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SOIL-VEGETATION RELATIONSHIPS ON AN INVOLUTED HILL, PLEISTOCENE MACKENZIE DELTA AREA, N.W.T.

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Soil-Vegetation Relationships on an Involuted Hill, Pleistocene Mackenzie Delta Area, N.W.T. submitted by Ross Hastings in partial fulfilment of the requirements for the degree of Master of Science

Don Gill

1934 - 1979

This thesis is dedicated to the memory of Don Gill, my supervisor and friend; a man who was proud to be a northerner and "one bad-ass dude."

ABSTRACT

The vegetation and soils of an involuted hill, a massive ground-ice landform on the Pleistocene Mackenzie Delta, were described quantitatively and qualitatively. The vegetation from 34 stands was classified into 5 community types (ct's) within 3 tundra groups, using minimum variance cluster analysis, principal components analysis and field observations. The Upland Tundra Group occurs on the outer ridges of the hill, on midslope positions and on the large ice-wedges of the hill's central plateau. There are 2 ct's in this group, the *Salix glauca*-*Lupinus arcticus* ct and the *Betula glandulosa*-*Vaccinium vitis-idaea* ct. Orthic Turbic Cryosols are the dominant soils in this group.

The Depressional Wetland Tundra Group occurs in wet, low-lying, sites in which the ground water is stagnant. This group is composed of 2 ct's. The Moss-*Eriophorum vaginatum* ct occurs in the large depressions between the outer ridges of the hill and in smaller ice-wedge polygon depressions; Gleysolic Static Cryosols are the dominant soil type. The Lichen-*Ledum palustre* ct occurs on well-developed, high-center polygons and in snowpack sites; Mesic or Humic Organic Cryosols are the most common soils in this ct.

The Lotic Wetland Tundra Group is found only along drainage channels that dissect the outer ridges of the hill. The *Salix pulchra*-*Alnus crispa* ct makes up this group.

All the ct's found on the involuted hill have been reported from other low arctic sites in North America. However, while the Depressional Wetland Tundra Group appears to be common along the arctic coastal plain, the Upland Tundra Group is more characteristic of the Foothills province of Alaska. It appears that the upland sites on involuted hills act as disjunct foothill elements.

Soils in depressional sites are water-logged. Plants that are able to translocate oxygen to their roots (e.g., *Eriophorum vaginatum*) or which root above the anaerobic portion of the solum (e.g., most ericads) dominate in the depressions. The drier, more aerated, soils of the Upland Tundra Group do not produce the gas exchange and toxicity problems encountered in the depressional sites. Therefore, in the upland sites, plants are able to freely root through the surface organic horizons.

Nutrient availability is a major factor which determines the location of the ct's on the involuted hill. A literature survey revealed that in tundra sites, deciduous shrubs have the highest nutrient demands, followed by graminoids, with evergreen shrubs being among the least nutrient-demanding of vascular plants. The *Salix glauca-Lupinus arcticus* ct is restricted to the sites of highest nutrient availability. *Betula glandulosa* is also most common in nutrient-rich stands.

Depressional stands are dominated by species adapted to nutrient--poor conditions. These species have low nutrient requirements and/or

are efficient in retaining nutrients they accumulate (e.g., *Ledum palustre*, lichens and mosses).

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1.0 INTRODUCTION

Previous synecological research in low arctic regions has attempted to establish the relationship between topography and vegetation patterns. Webber (1978), working in Barrow, Alaska, regarded microrelief, through its effects on drainage, as the principal control on the plant environment. Janz (1974) investigated soil and topographic relationships on the Pleistocene Mackenzie Delta and attempted to relate environmental patterns to the plant communities in the region as described by Corns (1974). Periglacial geomorphic features appear to be the major topographic elements along the arctic coastal plain; the distribution of plant communities is often related to the patterns of relief created by these features.

In the mid-1970's there was increasing resource exploration and anticipation of industrial development within the Mackenzie Delta region. Hence phenomena such as massive bodies of subsurface ice became of concern to engineers, geologists and ecologists, due to the high susceptibility to thermokarst erosion shown by these features. In response to this concern the Geological Survey of Canada initiated a number of studies to determine the nature and extent of massive ground ice features in the Mackenzie Delta region (e.g., Rampton and Mackay 1971, Rampton and Bouchard 1975). Geological investigations were conducted on two involuted hills in an attempt to determine the origin of these massive ground ice features. The Geological Survey also wanted baseline data on the plant communities which occur on the hills.

The general purpose of this thesis is to provide plant ecological information about an involuted hill which was studied by the Geological Survey. The principal objectives of this study are to: (1) provide an ecologically meaningful classification of the vascular plant community types (ct's) which occur on the involuted hill, (2) relate the ct's on the involuted hill to ct's found in other low arctic regions, and (3) attempt to provide some insight into edaphic factors affecting the distribution of the ct's on the involuted hill.

2.0 STUDY AREA

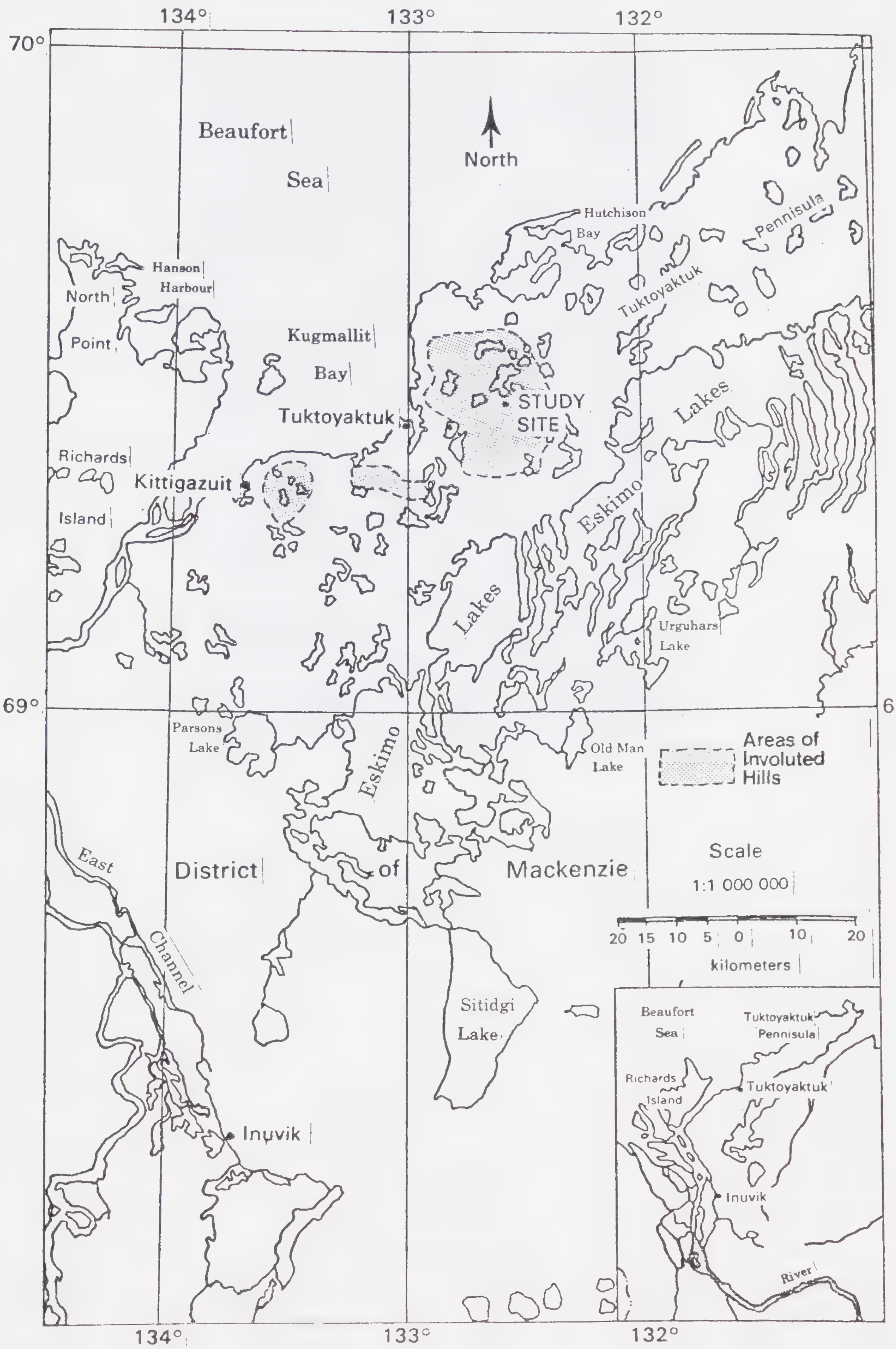
The involuted hills are concentrated in an approximately 500 sq km area which starts about 15 km east of the hamlet of Tuktoyaktuk. The involuted hill investigated in this project lies within the Geological Reserve created by the Geological Survey of Canada (Scott pers. comm. 1979) and is located at approximately $69^{o}30'$N Lat. and $132^{o}30'$W Long. (Figure 1).

2.1 Geological History

Involuted hills are large (1 x 2 km diameter and 30 m high) ice-cored mounds, in which both the ice wedge polygons and massive ground ice, which form the hills, have differentially melted out and partially slumped (Mackay 1963). A series of involutions on the hills has been created by the melting and slumping. On air photos, the involuted hills resemble "the wrinkled skin of a well-dried prune" (Mackay 1963) (Plate 1). The involutions "are curving to branching ridges, ranging up to several hundred yards in length, several score yards in width, and 20 feet in height" (Mackay 1963). Involuted hills along with pingos are important landform and ecological features on the Pleistocene Mackenzie Delta as they are the main elements of relief in the otherwise relatively flat, poorly drained, tundra terrain.

The area in which the involuted hills occur is underlain by the stratified sands and gravels of an ancient Pleistocene delta. These

Figure 1: Involuted hills on the Pleistocene Mackenzie Delta



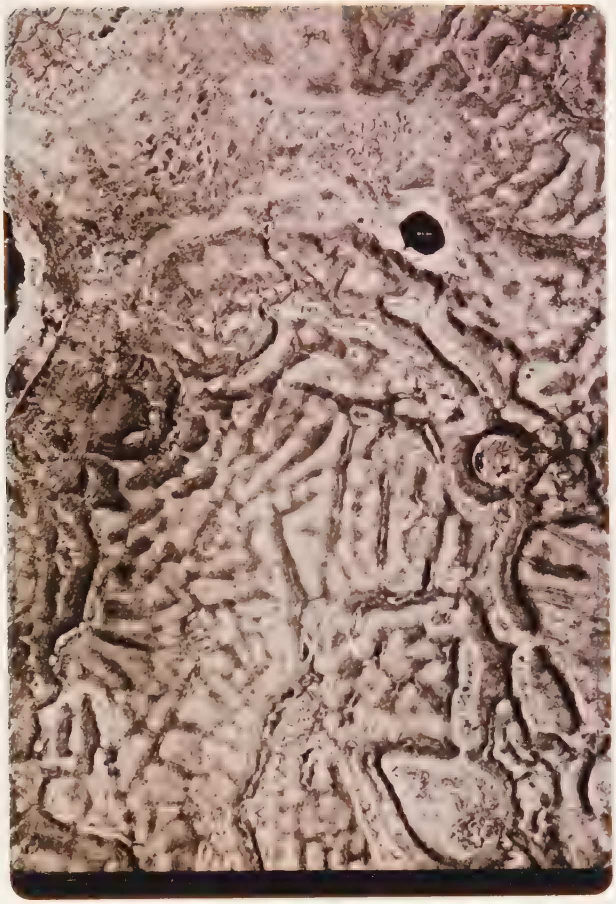


Plate 1 Air photo mosaic of the involuted hill study area. Dark tones are ridges or large ice wedges and are occupied by stands of the Upland Tundra Group. Lighter tones are stands of the Depressional Wetland Tundra Group.

deposits are found at a depth of approximately 35 m under the hills and 15 m under the surrounding area (Rampton and Mackay 1971, Rampton and Bouchard 1975, Scott, pers. comm. 1979). A 15-m thick layer of clayey diamicton lies over the sandy sediments. The diamicton appears to be a till but its surface has experienced slumping and is, therefore, colluvial in origin (Rampton and Bouchard 1975). Under the involuted hills, between the sand and gravel sediments and the diamicton, there is a zone of highly convoluted massive ground ice. These ground ice masses are responsible for the relief of the involuted hills; if they were to melt out the hills would collapse to the level of the surrounding terrain.

The basal sand and gravel deposits appear to be of glacio-fluvial origin from a proglacial delta that prograded into a marine environment (Rampton and Bouchard 1975). The overlying till is believed to be from an early Wisconsin advance of the Laurentide ice-sheet. An early- or pre-Wisconsin date is, therefore, ascribed to the sandy sediments. Radiocarbon dates from the area are beyond the range of C^{14}, thereby indicating that the till deposits are greater than 40,000 years old (Mackay et al. 1972). Rampton (1982) calls this early-Wisconsin advance the Buckland Glaciation. This glaciation covered the Mackenzie Delta area to the Richardson Mountains in the west and reached its northern limit along a line from Kugmallit Bay across the Tuktoyaktuk Peninsula to Liverpool Bay (Forbes 1980). The late-Wisconsin glaciation apparently did not cover the Tuktoyaktuk Peninsula area; hence the area has probably been unglaciated for at least 40,000 yrs (Forbes 1980, Rampton 1982).

The massive ground ice under the till formed subsequent to glaciation for it is not composed of glacial ice (Rampton 1973). It has been proposed that the water which formed the massive ground ice came from the melting continental glacier, flowing through the sandy sediments under the till driven by a hydraulic gradient created by the weight of the retreating glacier (Rampton 1973). Massive segregation ice between the till and sandy sediments formed under the influence of the periglacial climates which developed subsequent to glaciation. The involuted hills have probably been in existence since the retreat of the late-Quaternary continental glacier (40,000 yrs). Rampton (1973) states that the Tuktoyaktuk Peninsula was fairly stable geologically for the remainder of the Quaternary.

During a postglacial period from about 11,500 to 3,600 B.P. the climate improved and at about 8,000 B.P. was warmer than present conditions (Ritchie and Hare 1971, Ritchie 1972). During this period there was extensive thermokarst activity and the hills probably took on their present involuted appearance through slumping caused by melting of ice wedges and differential exposure of massive ground ice. Thermokarst activity appears to have slowed when climatic conditions started to deteriorate at 5,000 yr B.P. (Rampton 1973). Thus it seems that the involuted hills have been in existence for about 40,000 yrs and have attained their present form within the past 5,000-10,000 yrs.

2.2 Climate

The study area has a maritime tundra climate (Burns 1973). The

nearby hamlet of Tuktoyaktuk has a short frost free period (56 days) and low annual precipitation (138 mm) (Figure 2). However, this frost free period is about 3 weeks longer than that at Barrow and Tuktoyaktuk receives 30% more precipitation over the year (Webber 1978). Tuktoyaktuk and Barrow have mean annual temperatures of -10.9 and -12.5^{o}C, respectively, and a mean daily maximum temperature of the warmest month of 15.2 and 7.2^{o}C respectively (Webber 1978, Canada Climate Program 1982). The warmer, wetter climate of Tuktoyaktuk is probably due to the moderating influence of the Mackenzie River. The river brings in warm water from southern areas causing a relatively early breakup and more moderate temperatures along the coast (Gill, pers. comm. 1977).

2.3 Soils

The most prominent features of the soils on the Tuktoyaktuk Peninsula are the presence of permafrost near the surface combined with intense cryostatic activity. Permafrost inhibits drainage through the soil profile and subsequently seasonal waterlogging is common in the lower part of the active layer (Zoltai and Tarnocai 1974). This inhibition of drainage creates anaerobic conditions and, subsequently, gleyed horizons in the mineral part of the solum are common.

Earth hummocks, which are created by frost activity, are the dominant micro-topographic features in the region. Soils which develop under these hummocks are extremely cryoturbated with the upper

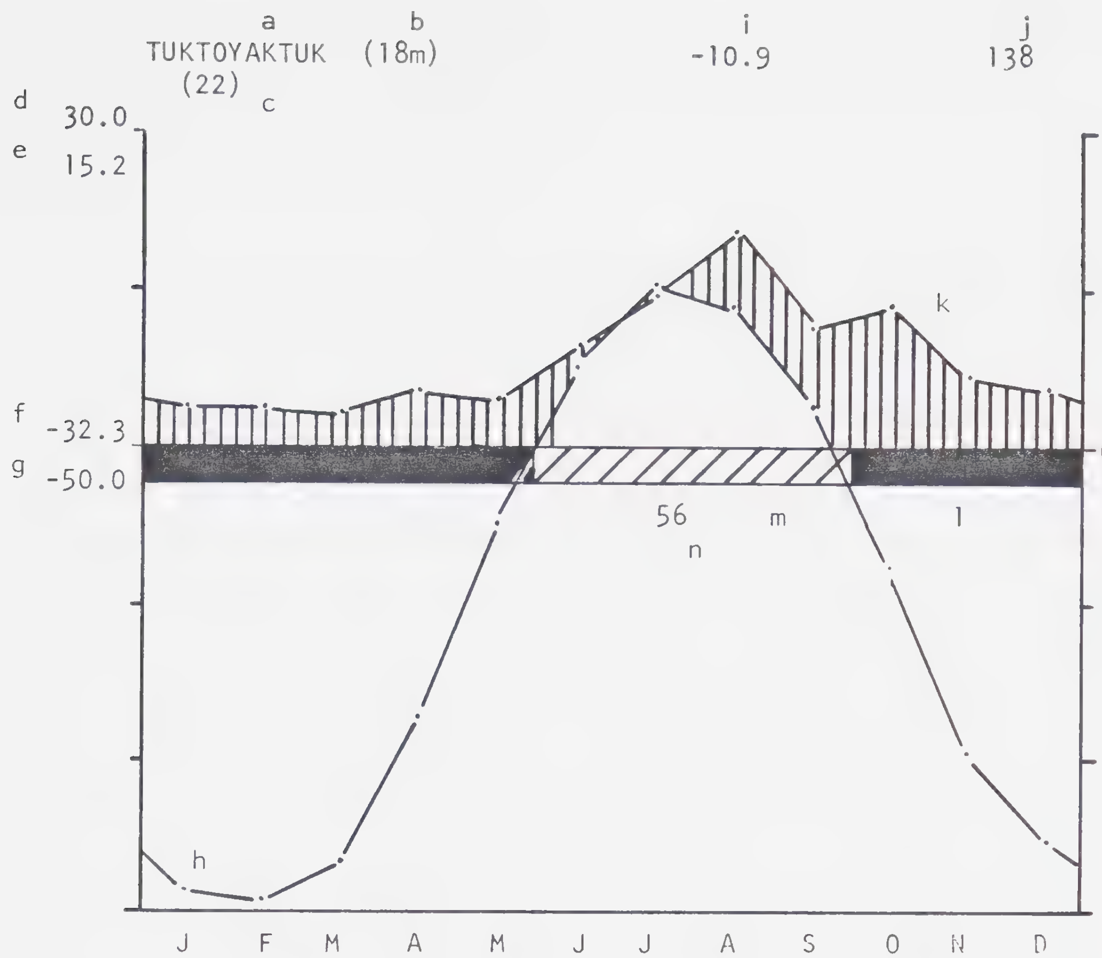


Figure 2. Climatic diagram for Tuktoyaktuk, N.W.T.(after Walter 1973) on the basis of data from the Canadian Climate Program (1983). Abscissa: months (Jan.-Dec.); ordinate: 1 division = 10 C or 20 mm precipitation. a,station name; b,elevation; c,duration of observation (yrs); d,highest recorded temperature C; e,mean daily maximum temperature of the warmest month; f,mean daily minimum temperature of the coldest month; g,lowest recorded temperature; h,curve of mean monthly temperature; i,mean annual temperature; j,mean annual precipitation; k,curve of mean monthly precipitation; l,months with mean daily temperature below 0 C; m,months with absolute minimum temperature below 0 C; n,mean duration of frost free period in days.

horizons commonly being broken by frost action and parent material being forced to the surface (Zoltai and Tarnocai 1974). Profile development is weak in these soils.

Zoltai and Tarnocai (1974) report that Turbic Cryosols dominate in the Pleistocene Mackenzie Delta Region while Clayton et al. (1972) report the dominant soils are Cryic Gleysols with subdominant Cryic Regosols. The Canadian System of Soil Classification as devised by the Canada Soil Survey Committee (1978) resolves these two points of view. Under this system the dominant soils of the region would now be classified as Gleysolic Turbic Cryosols with Regosolic or Orthic Turbic Cryosols being subdominant. The Gleysolics will tend to be more common in depressional positions while the Regosolics and Orthic Turbics will be more common in the somewhat better drained upland sites. Clayton et al. (1972) also report significant inclusions of fibrisols on the Tuktoyaktuk Peninsula. Under the Canadian System of Soil Classification (1978) these soils would now be contained within the Organic Cryosol Great Group. These Organic soils are common in drained lake basins and in other locations which have well developed high-center polygons.

3.0 METHODS

3.1 Field Research

In this thesis 'stand' refers to a particular example of vegetation which was sampled. 'Community type' refers to a grouping of similar stands. Representative stands for vegetation sampling were chosen from low-altitude, orthophoto maps of the involuted hill (Geological Survey of Canada 1977). Stands to be sampled were chosen on the basis of differences in tone and texture on the orthophoto map and on differences in topographic position. Transects 50 m in length were located in the field from the orthophoto maps. The transect was placed in the center of the stand as close to parallel to the long axis of the stand as possible. Two 1 m^2 quadrats were sampled within each 10 m section of the transect. The location of the quadrats within the 10 m section were chosen from a three-digit random numbers table. The first digit determined whether the first quadrat was on the right side (even number) or left side (odd number) of the transect. The second quadrat was always on the opposite side of the transect from the first quadrat. The second digit indicated the position of the first quadrat, in meters, from the start of each 10 m section. The third digit indicated the position of the second quadrat from the start of the section. This procedure was repeated for all five 10 m sections in the transect, yielding ten randomly stratified, 1 m^2 quadrats for each of the stands. Quadrats were placed 1 m from the transect line in order to avoid sampling vegetation which had been crushed during establishment of the line. Between June 22 and July

31, 1980, a total of 35 stands were sampled. One transect was eliminated from the data-set as it included both high- and low-center polygon community types and therefore was distinctly heterogeneous.

Within each quadrat live vascular plant cover was estimated by species and assigned a cover class value (Table 1). Covers of both lichens and mosses were estimated for their entire taxonomic complex, i.e., they were not separated into species. The height of the tallest plant species in each quadrat was also recorded. Surface conditions were described in each quadrat including the areal extent of hummocks, interhummock depressions (hollows), and tussocks. Specimens of all vascular plant species that were found on the involuted hill were collected. Voucher specimens were deposited in the Northern Forest Research Centre Herbarium (NFRC) in Edmonton.

During a dry period from the 17th to the 31st of July soils were sampled in 18 of the 35 vegetation stands. The soil sample sites were chosen on the basis of drainage regime and vegetation. Five pits 5 m apart were dug in each of the sampled stands. At 3 of the pits, the following data were recorded: 1) soil temperature, 2) frost depth, 3) thickness of organic and clay horizons, 4) geomorphic features, and 5) dominant vegetation. At the other 2 pits the above data were collected and, additionally, each horizon was identified and its thickness, texture, structure, color and lower boundary form were noted. Depth to frost was measured by inserting a steel probe into the ground until it contacted the frost table, withdrawing the probe and then measuring the depth of penetration along the probe. Field

Table 1. Midpoints assigned to cover class values; based on % of ground covered by a species in each quadrat.

Cover Class Value	% Cover Range	Midpoint
+	rare	.1
1	< 1	.5
2	1 - 5	3
3	6 - 10	8
4	11 - 25	18
5	26 - 50	38
6	51 - 75	63
7	76 - 90	83
8	91 - 95	93
9	96 - 100	98

descriptions of the soil profiles followed Dumanski (1978). Samples for soil moisture, texture and nutrients were taken from each of the major horizons (< 5 cm) in each of the soil pits and placed into heavy gauge plastic bags which were then heat-sealed. This collecting method followed Zoltai (1980). In transit to Edmonton, soils from 3 of the stands were lost and, therefore, moisture, texture and nutrients were determined for 15 stands.

3.2 Laboratory Procedures

The cover-class values assigned to each species were converted to midpoints (Table 1). Averaging of the midpoints for each species in the 10 quadrats gave a mean cover for that species in the stand. Similarity coefficients for the $n(n-1)/2 = 561$ stand pairs (distance matrix in Appendix I) were computed as squared euclidian distance (Wishart 1978). Wards method of minimum-variance cluster analysis (Wishart 1978) was used to classify the stands into community types using Wishart's CLUSTAN 1-C program-set. Since lichens and mosses had several species in each stand but were recorded as single taxonomic units, they were masked from the final analysis. However, comparison between runs in which lichens and mosses were masked and un-masked showed no important difference in stand classification.

A principal components analysis (PCA) was done in conjunction with the above technique in order to help synthesize the cover value data from the stands so that they could be grouped into community types. PCA is a useful classification technique when the underlying

environmental factors controlling the distributions of species is not known. Mathematical details for the calculation of PCA can be found in Orloci (1975) and Pielou (1977). Simple summaries of the principles of PCA are given by Gauch (1977, 1982).

A single PCA was run using untransformed cover data from the 34 stands. The analysis was carried out using the CLUSTAN 1-C program package of Wishart (1978). Since the number of species and stands were relatively small there were no problems encountered in program restrictions and therefore cover values for all species were included in the analysis. A single two-dimensional ordination of all the stands on the hill was constructed using the first and second principal components as the x and y axis respectively.

Species names follow Hultén (1968). Data sheets for the plant community survey, based on Corns (1974), were drawn up before the new flora for the region (Porsild and Cody 1980) was published. Differences in the classification of certain species groups between the two nomenclatural authorities make translation to the new system difficult.

Soils were collected in heavy plastic bags and heat-sealed (see 3.1); this method yields good results for physical properties and nutrient analysis (Zoltai 1980). However, due to organic matter decomposition in the sealed environment, the pH values of the samples may have decreased towards the acidic side of the scale. The pH values cited in this text are, therefore, probably lower than those of

fresh soil samples. Also, though the bags were heat-sealed, there may have been moisture loss from some of the samples. The samples were stored in a very dry laboratory; the vapour pressure of the air in the bags would have been higher than that of the surrounding air. Diffusion of air from some of the bags is evidenced by the bags being drawn tight around the soil sample. Some moisture from the soil was probably lost during diffusion from the bag. Since there is no measure of the moisture loss from the bags, loss was assumed to be uniform between the samples. Reported moisture contents are, therefore, minimum values; field moisture was probably higher. Due to initially inadequate storage and processing facilities, partial decomposition of the samples could not be prevented. Therefore, the available nutrient values are meaningful only in relation to other samples from this study and should not be uncritically compared to data from other research.

Since bulk density was not determined in the field, nutrient analysis was initially calculated on a per unit weight rather than volume basis. Because the organic soil samples are very light in comparison to the mineral soil samples, however, this method produces results which make the organic samples appear to be much more nutrient-rich than the mineral samples. In order to compensate for this problem equal weights of dried samples from the organic and mineral portion of each pit were weighed and then their volumes measured under equal compaction pressure. A conversion factor based on volume was determined for each sample in order to express the nutrient value of all soils on a unit-volume basis. Even with this

conversion nutrient values of the organic samples appear to be too high. The higher values may be due to breakage of the organic matter in processing, thus yielding higher weight per volume than would have occurred in untreated fresh samples.

Field soil moisture content was determined by weighing a sample of the soil, drying it at 105^{o}C for 24 hours, and then re-weighing it (Eilers 1976). Laboratory analysis on the 2 mm fraction included: pressure plate extraction to determine moisture retention at -1/3 and -15 bars (Eilers 1976); particle-size analysis by the pipette method (Green 1976); pH by calcium chloride (Osborne 1976); and organic matter by the wet oxidation method of Walkley and Black (1934). Exchangeable cations were determined by extraction with ammonium acetate and by atomic absorption spectrophotometry (Chapman 1965). Total phosphorus was determined by sodium carbonate fusion (Atkinson *et al.* 1958) and total nitrogen by a semi-micro Kjeldahl method (Bremer 1965). Statistical analysis of soils data were conducted by a Students t-test at 95%.

4.0 RESULTS

4.1 Vegetation

4.1.1 Cluster Analysis

A cluster analysis dendrogram was used to classify the plant community types (ct's) on the involuted hill (Figure 3; see methods, 3.2). The classification is quantitative as it is based on the cover of plant species and the plant community types are thus distinguished in terms of both species composition and species structure. The dendrogram contains 3 primary clusters which effectively separate the community types into upland sites on the left and lotic and depressional sites on the right. These 3 clusters are fused at a coefficient of 150.911. Five secondary clusters, corresponding to community types, are distinguished at a coefficient of 56.306. The primary upland cluster consists of 2 secondary clusters which include (1.) stands dominated by *Salix glauca* (1,8,10,12,16,18,25) and (2.) *Betula glandulosa* (2,4,6,13,14,17,20,21,27,32,35). The primary depression cluster consists of 2 secondary clusters. The first cluster (3.) is dominated by moss species, predominantly *Sphagnum*; shrubs have notably low cover values (stands 3,5,9,11,15,19,28,29,32). The second cluster (4.) (stands 7,22,23,24,30) is dominated by lichens and is quite heterogeneous in terms of composition. Ordination reveals that stands 22 and 24 are also closely related to the preceding cluster (see below). Stands of the final, lotic, cluster (5.) are dominated by *Salix pulchra* (26,33).

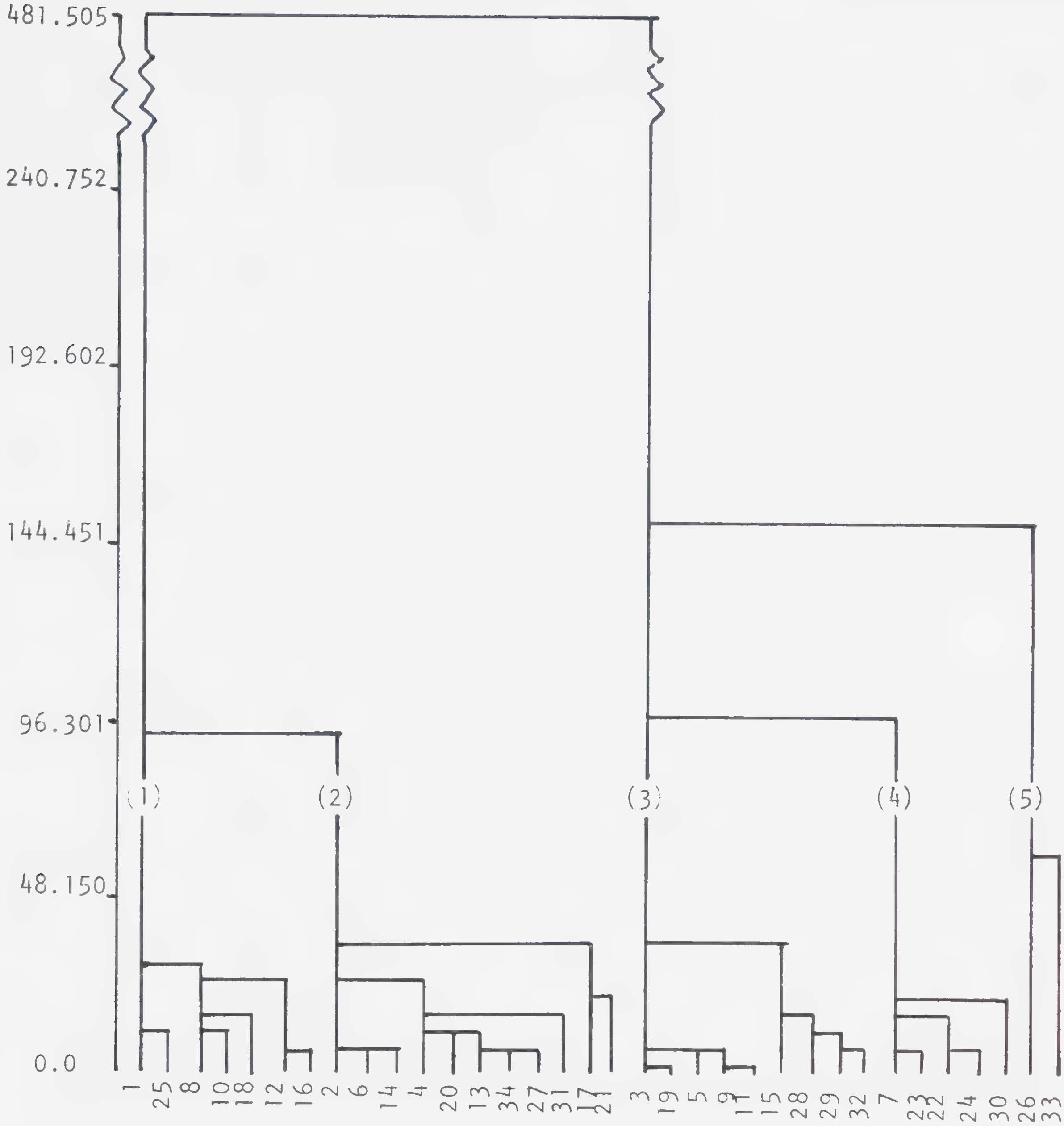


Figure 3. Quantitatively-based cluster dendrogram showing classification hierarchy of stands found on the involuted hill. Bracketed numbers indicate community types recognized at the 56.306 coefficient.

4.1.2 Ordination

Species cover data were used to construct an indirect ordination of the involuted hill stands (Figure 4; see 3.2). Generally, the results of the ordination supported the community classification of the cluster analysis, but there was some deviation. Again, upland and depressional sites were clearly separated with upland stands grouped to the left of the vertical axis and depressional stands grouped to the right. Also, with the exception of stands 2,6,13,17 and 21, shrub-dominated stands lie above the horizontal axis while non-vascular-dominated stands lie below this axis.

Stands of the ct dominated by *Salix glauca* (1.) tend to lie to the extreme left of ordination. However, stands 1 and 10 of this ct lie within the *Betula glandulosa* ct sector of the ordination, which lies slightly to the right of the *Salix glauca* sector. This minor overlap of stands shows the compositional similarity of the two community types, but since the *Betula* stands form a tight group with no intrusion into the main *Salix glauca* sector the cluster analysis was not changed. Also, the *Betula* group may separate from *Salix* #1 and 10 on a third axis.

Stands of the moss ct lie in the lower right portion of the ordination diagram. Stands from the lichen ct which have developed on high-center polygons form a separate group slightly to the left of the moss ct. However, stands 22 and 24 of the lichen ct are found within the moss cluster; both of these stands are in snowbank sites and have

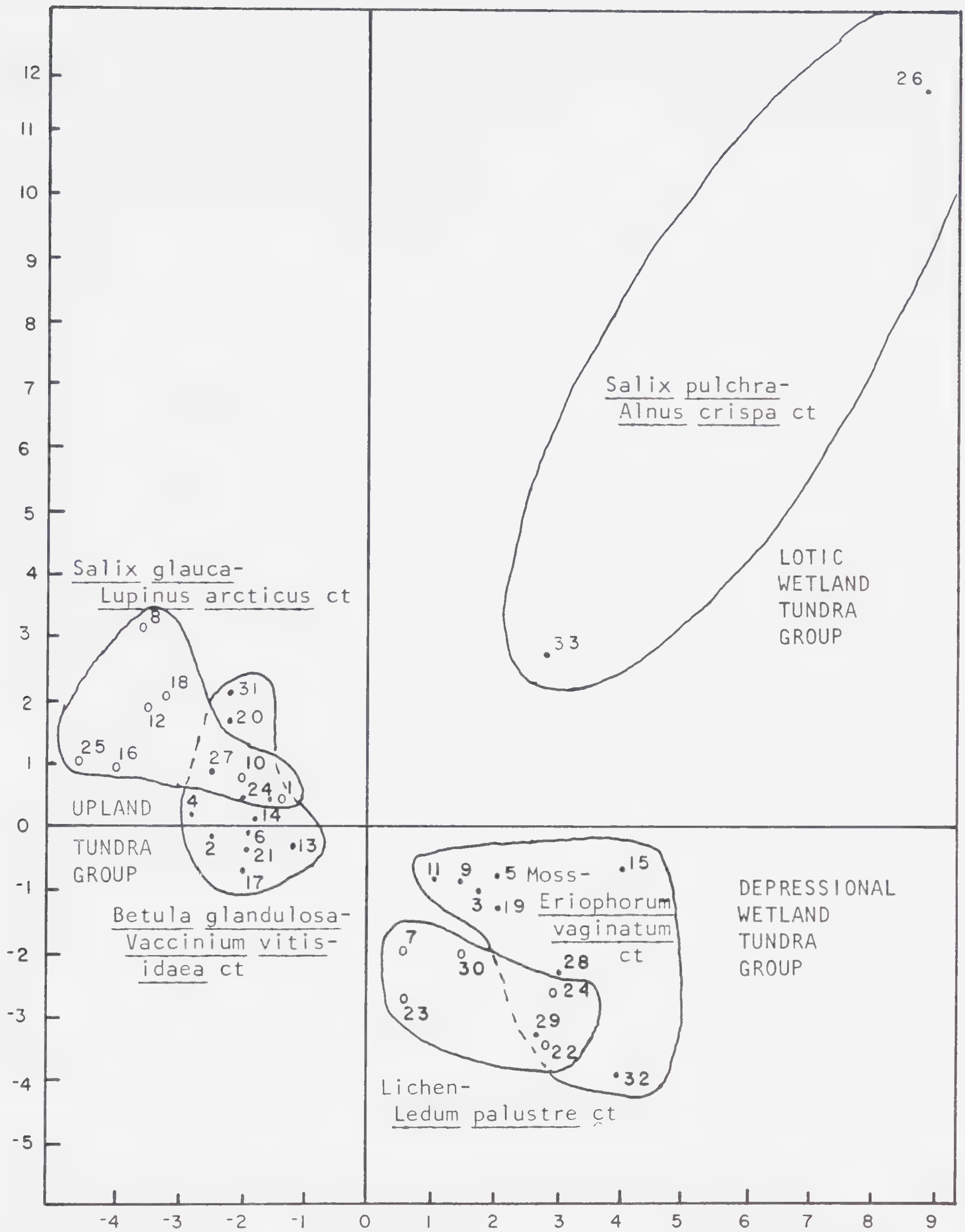


Figure 4. Principal components analysis ordination of the 34 stands, 5 tundra community types, and 3 tundra groups of the involuted hill study area.

high covers of both lichens and mosses, the dominants in the two community types. Since snowbanks and high-center polygons both have severe environmental conditions, it was decided to leave stands 22 and 24 within the lichen ct rather than linking them to the Moss-*E. vaginatum* ct.

The *Salix pulchra* ct (5.) occupies the upper right portion of the ordination. The wide spacing between the stands in the ordination diagram combined with the relatively high coefficient at which they link in the cluster analysis indicates that there is much compositional variation between these 2 stands. Linkage of these 2 stands appears to be based primarily on having in common species that are absent in all other stands (e.g. *Alnus crispa*), and having high covers of species rare in other stands (e.g. *Salix pulchra*). Because only two lotic sites were sampled the stands were grouped into a single ct. Had more sites been sampled it is likely that more than one lotic ct would have been distinguished.

4.1.3 Classification

By use of cluster analysis, supported by field observation, the vegetation of the involuted hill can be classified into 2 major topographic groups and 5 community types (Table 2). The ct's were given binomial names using two dominant character species. The first name was always the dominant species of the ct. The second name was chosen on the basis of that species having a high cover value but it also had to have its maximum concentration in the community type.

Table 2. Classification of the plant community groups and types (ct's) on the involuted hill, Tuktoyaktuk Peninsula, N.W.T.

I. Upland Tundra Group

1. *Salix glauca*-*Lupinus arcticus* ct (1,8,10,12,16,18,25)*
2. *Betula glandulosa*-*Vaccinium vitis-idaea* ct (2,4,6,13, 14,17,20,21,27,31,34)

II. Depressional Wetland Tundra Group

3. Moss-*Eriophorum vaginatum* ct (3,5,9,11,15,19,28,29,32)
4. Lichen-*Ledum palustre* ct (7,22,23,24,30)

III. Lotic Wetland Tundra Group

5. *Salix pulchra*-*Alnus crispa* ct (26,33)

* Stand numbers

This generally follows one system of nomenclature outlined by Mueller-Dombois and Ellenberg (1974) and closely follows Kuchar (1975), Hrapko and LaRoi (1978), and Mortimer (1978).

4.1.4 Community Descriptions

4.1.4.1 Upland Tundra Group

1. *Salix glauca-Lupinus arcticus* community type (stands 1,8,10,12,16,18,25) (Table 3, Plate 2)

The *Salix glauca-Lupinus arcticus* ct occupies the large outer ridges of the involuted hill, midslope positions and also the rims of large, mineral-based, ice-wedges which occur on the central plateau. This ct is found 1.5-5.0 m above local depressions and is moderately well drained to somewhat poorly drained. The perennially dry nature of these stands is indicated by abundant ground squirrel burrows.

Salix glauca (43% cover) and *Betula glandulosa* (32%) are the dominant species in this ct. However, while *S. glauca* is at its maximum cover in these stands, *B. glandulosa* is slightly below its mean overall cover on the hill. *Empetrum nigrum* is at its highest cover (25%) in this ct and preferentially occupies the abundant earth hummocks. The herbs *Lupinus arcticus*, *Pyrola grandiflora* and *Senecio lugens* are also most abundant in this ct. By contrast, mosses are at their lowest cover (14%) on the hill, being found principally in hollows around earth hummocks. Lichens (11%) are also well below

Table 3. Species cover values for the Salix glauca-Lupinus arcticus ct on the involuted hill.

Stand no.	1	8	10	12	16	18	25
$\bar{x}$ cover %							
vascular	123.1	157.0	181.7	158.6	167.3	204.5	162.4
moss	4.3	6.0	9.5	10.5	15.5	40.5	11.0
lichen	3.7	15.0	9.5	9.0	11.0	16.0	11.0
No. Vascular species	13	22	22	23	21	21	22
Cover Vascular species							
Salix glauca	28.7	41.5	31.5	43.5	53.0	54.5	46.5
Salix phylicifolia	6.3	--	--	--	--	--	--
Betula glandulosa	16.6	43.5	40.0	42.5	33.0	32.0	13.8
Dryas integrifolia	--	--	--	0.02	--	--	--
Empetrum nigrum	24.4	24.4	44.0	9.8	11.9	35.6	27.0
Ledum palustre	14.4	1.7	6.7	7.0	15.1	14.2	17.7
Cassiope tetragona	--	--	--	--	--	0.02	--
Arctostaphylos alpina	--	--	1.8	0.8	0.06	--	0.3
Arctostaphylos rubra	--	4.4	0.6	0.01	--	1.8	0.3
Vaccinium vitis-idaea	9.8	16.2	26.0	21.5	25.5	21.5	21.0
Vaccinium uliginosom	--	5.4	1.1	--	--	1.8	--
Stellaria spp.	0.05	0.5	0.1	0.1	0.2	0.8	1.0
Pulsatilla patens	--	--	--	--	--	--	0.3
Cardamine hyperborea	--	0.5	0.3	--	--	0.7	--
Draba cinerea	--	--	--	--	0.05	--	0.05
Potentilla hookeriana	--	--	--	--	0.05	--	--
Lupinus arcticus	7.0	7.7	9.7	17.0	21.0	9.8	20.2
Conioselinum cnidifolium	--	0.4	--	0.1	0.2	--	0.01
Pyrola grandiflora	13.9	4.9	7.0	9.9	4.4	23.5	8.2
Pyrola secunda	1.8	1.6	2.7	3.2	0.60	3.9	2.4
Castilleja elegans	0.01	--	--	--	0.01	--	0.9
Pedicularis lapponica	--	--	--	0.01	--	--	--
Pedicularis labradorica	--	--	0.9	00	00	0.05	0.3
Pedicularis langsdorfii	--	--	0.6	--	--	--	--
Pedicularis capitata	--	1.4	1.1	0.9	--	1.2	0.6
Pedicularis kaneii	--	0.01	0.6	0.3	--	0.01	--
Petasites frigidus	--	0.6	2.5	0.4	0.6	2.2	0.9
Senecio atropurpueus	0.02	1.1	0.8	0.1	0.05	0.4	--
Senecio lugens	--	0.3	--	1.0	0.9	0.2	0.1
Hierochloe alpina	--	--	0.4	0.02	0.01	0.3	0.2
Arctagrostis latifolia	--	0.3	1.8	0.03	0.01	--	0.4
Poa spp.	--	--	--	--	0.05	0.01	0.2
Kobresia myosuroides	--	0.3	--	--	--	--	--
Carex scirpoidea	--	0.3	--	--	--	--	--
Carex rupestris	0.10	--	--	--	0.60	--	--
Carex bigelowii	--	0.01	1.5	0.06	--	--	--
Carex capillaris	--	--	--	0.4	--	--	--

Plate 2 A *Salix glauca*-*Lupinus arcticus* stand on a well-drained outer ridge of the involuted hill. Stands of this ct are easily identified in the field by the abundance of the colorful *Lupinus arcticus*. Range pole segments are 20 cm.

their mean cover value for the hill.

2. Betula glandulosa-Vaccinium vitis-idaea community type (stands 2,4,13,14,17,20,21,27) (Table 4, Plate 3)

The Betula glandulosa-Vaccinium vitis-idaea ct has the same habitat characteristics as the S. glauca-L. arcticus ct. It also has the same relief (1.5-5.0 m) above local depressions. However, it has significantly sandier soils and therefore may have somewhat better drainage. Ground squirrel burrows are again abundant.

Betula glandulosa (48%) reaches its highest cover value in this ct and is the dominant species. Salix glauca (28%) also has a high cover value. The dominant heath on the involuted hill, Vaccinium vitis-idaea is at its maximum coverage (28%) in this ct. Like the other upland ct this one has a low cover of mosses (14%) but lichens have increased to 17%, equal to their mean value for the hill.

4.1.4.2 Depressional Wetland Tundra Groups

All low-lying ct's on the involuted hill are characterized by a much lower cover of Salix glauca, a moderately lower cover of Empetrum nigrum and a significantly higher cover of mosses, cf. the upland cts.

Table 4. Species cover values for the Betula glandulosa-Vaccinium vitis-idaea ct on the involuted hill.

Stand no.	2	4	6	13	14	17	20	21	27	31	34
$\bar{x}$ cover											
vascular	182.2	126.9	188.6	158.3	175.7	145.8	172.3	192.4	192.0	169.0	169.7
moss	5.5	9.0	6.5	6.7	9.5	18.5	20.0	51.0	8.7	9.5	14.7
lichen	13.5	10.5	12.0	15.4	13.0	24.5	16.0	34.0	19.2	14.0	13.2
No. Vascular species	13	15	15	15	22	17	24	21	22	21	21
Cover Vascular species											
Salix glauca	36.2	25.0	29.2	30.5	25.0	16.4	20.2	13.9	38.0	35.5	35.0
Salix pulchra	--	--	0.8	--	0.01	--	1.8	--	--	--	--
Betula glandulosa	54.2	39.1	61.2	43.0	57.5	46.8	44.0	43.5	42.2	48.0	45.0
Empetrum nigrum	19.7	13.2	23.2	24.7	26.7	1.9	26.0	24.2	25.5	9.6	18.5
Ledum palustre	23.2	7.9	31.0	20.0	16.2	16.6	19.2	38.5	22.0	23.5	14.5
Arctostaphulos alpina	--	1.1	--	--	0.8	--	--	0.8	1.1	--	--
Arctostaphulos rubra	--	--	0.3	--	--	--	2.6	--	0.01	--	0.6
Vaccinium vitis-idaea	33.5	20.0	28.0	24.0	33.0	46.2	21.0	37.0	30.0	10.5	23.0
Vaccinium uliginosum	--	--	--	--	1.8	--	--	14.3	00	9.2	--
Polygonum bistorta	0.01	0.01	--	--	--	--	--	--	--	--	--
Stellaria spp.	0.4	0.4	0.3	0.3	0.2	0.4	0.9	2.2	0.1	0.4	0.2
Anemone richardsonii	--	--	--	--	--	--	--	--	--	0.4	--
Pulsatilla patens	--	0.3	--	--	--	--	--	--	--	--	--
Cardomine hyperborea	--	--	--	--	--	--	0.6	1.0	--	0.6	--
Draba cinerea	--	--	--	--	--	--	--	--	0.05	--	--
Rubus chamaemorus	0.05	0.01	--	0.6	0.3	--	--	--	0.3	--	0.3
Potentilla hookeriana	--	0.05	--	--	--	--	--	--	--	--	--
Lupinus arcticus	6.2	14.7	6.2	10.0	4.2	8.2	6.9	2.7	9.5	12.0	16.5
Conioselinum cnidifolium	0.07	--	--	0.02	0.05	--	0.05	--	--	--	--
Pyrola grandiflora	7.5	4.1	5.0	0.9	3.2	1.1	5.2	3.3	9.7	11.2	5.2
Pyrola secunda	1.2	--	1.8	1.4	1.5	1.4	2.6	2.3	2.6	5.0	3.6
Castilleja elegans	--	--	--	--	--	0.3	00	00	00	0.01	--
Pedicularis lapponica	--	--	--	--	--	--	--	0.01	--	--	--
Pedicularis labradorica	--	0.05	--	--	--	--	--	0.3	--	--	0.01
Pedicularis capitata	--	--	--	--	0.3	--	2.4	0.4	1.4	0.6	0.3
Pedicularis kaneii	--	--	0.05	--	0.01	0.3	0.1	0.01	0.01	--	0.01
Petasites frigidus	--	--	1.2	1.0	3.2	0.6	2.8	--	6.2	0.4	3.9
Senecio atropurpureus	0.01	--	--	--	0.3	--	0.5	3.8	00	0.6	0.1
Senecio lugens	--	--	--	--	0.2	--	0.3	--	0.1	0.6	--
Hierochloe alpina	--	--	0.3	0.3	--	2.4	1.7	1.2	0.6	--	0.3
Arctagrostis latifolia	--	--	--	1.2	0.1	2.9	1.5	2.1	1.8	0.4	1.3
Trisetum spicatum	--	--	--	--	--	0.01	--	--	--	--	--
Poa spp.	--	--	--	0.4	0.05	--	0.01	0.1	0.4	0.5	1.0
Eriophorum vaginatum	--	--	--	--	--	--	1.8	--	--	--	--
Carex rupestris	--	--	--	--	--	0.3	0.8	--	--	--	--
Carex bigelowii	--	1.0	0.1	--	1.1	0.01	9.2	0.8	0.4	--	0.4
Luzula confusa	--	--	--	--	--	--	--	--	0.05	0.01	0.01
Dupontra fisheri	--	--	--	--	--	--	--	--	--	0.01	--

Plate 3 A Betula glandulosa-Vaccinium vitis-idaea stand on a large ice wedge of the involuted hill's central plateau. The stand is bounded on both sides by Moss-Eriophorum vaginatum stands. Pingos and a second involuted hill are in the background.

3. Moss-*Eriophorum vaginatum* community type (stands 3,5,9, 11,15,19,28,29,33) (Table 5, plate 4)

The Moss-*Eriophorum vaginatum* ct occurs in the depressions between the outer ridges of the hill and in the smaller ice-wedge polygon depressions. Its low-lying topographic position results in its having poor drainage and relatively wet conditions. In these stands mosses (38%), notably peatmosses, predominate. These mosses grow in the flat, low-lying, ground between *E. vaginatum* tussocks and scattered earth hummocks. *Eriophorum vaginatum* is the dominant vascular plant in this ct with a cover of 26%; it has a cover of less than 2% in the other ct's. Another prominent sedge is *Carex bigelowii*. It is found mostly on the scattered earth hummocks but still attains a cover of 10%, its second highest on the hill. *Betula glandulosa* (16%) is at its lowest cover on the hill and *Salix glauca* (2%) is rare. The herbs common in upland stands, principally *Lupinus arcticus* and *Pyrola grandiflora*, are very rare (< 0.5%) in the Moss-*E. vaginatum* ct. Lichens at 16% are near their mean cover for the hill.

4. Lichen-*Ledum palustre* community type (stands 7,22,23,24) (Table 6, Plates 5,6)

Like the Moss-*E. vaginatum* ct, the Lichen-*Ledum palustre* ct is found only in depressional sites. Most commonly this ct is found on well-developed, high-center polygons which have formed in the depressions. The massive ice-wedges in these sites disrupt drainage, thereby creating the wettest conditions on the hill. This ct also

Table 5. Species cover values for the Moss-*Eriophorum vaginatum* ct on the involuted hill.

Stand no.	3	5	9	11	15	19	28	29	32
$\bar{x}$ cover									
vascular	104.9	104.5	105.8	117.3	124.0	125.5	130.0	111.8	95.5
moss	35	31.2	32.0	27.0	42.5	47.0	50.5	36.0	9.5
lichen	20.5	13.2	11.2	20.0	0.8	14.0	14.5	31.5	14.0
No. Vascular species	17	24	25	19	21	24	18	21	16
Cover Vascular species									
Salix reticulata	--	--	--	--	0.3	--	--	--	--
Salix fuscescens	--	--	--	--	--	--	0.4	--	--
Salix glauca	3.3	2.7	3.6	6.6	--	3.0	--	0.01	--
Salix pulchra	0.1	2.4	1.8	1.7	16.2	4.4	0.3	0.6	2.1
Betula glandulosa	18.7	18.2	17.0	21.5	14.5	22.0	11.7	16.5	7.6
Dryas integrifolia	--	0.05	0.01	--	--	--	--	--	--
Empetrum nigrum	15.0	14.2	9.5	13.5	13.0	17.5	12.5	8.4	10.5
Ledum palustre	15.0	9.2	10.5	13.0	5.2	14.5	18.0	21.0	15.5
Andromeda polifolia	--	0.01	--	--	0.05	--	--	--	--
Arctostaphylos alpina	--	5.2	0.6	1.1	3.7	1.2	3.2	3.8	6.6
Arctostaphylos rubra	2.3	--	--	--	--	--	1.8	0.01	--
Vaccinium vitis-idaea	17.5	15.7	22.5	18.5	9.2	15.5	17.0	17.0	19.0
Vaccinium uliginosum	--	6.4	1.8	--	11.1	0.3	--	--	--
Tofieldia pusilla	--	--	--	--	--	--	--	--	0.05
Rumex arcticus	--	--	--	--	--	0.01	00	0.02	--
Stellaria spp.	0.1	0.3	0.07	0.05	0.01	0.4	--	0.05	--
Cardomine bellidifolia	0.01	--	--	--	--	--	--	--	--
Cardomine hyperborea	--	--	0.2	0.07	0.07	0.3	--	--	--
Rubus chamaemorus	0.4	0.01	0.08	--	1.1	00	4.4	3.4	4.5
Lupinus arcticus	--	0.8	0.8	0.6	--	0.7	--	--	--
Pyrola grandiflora	0.8	4.0	2.2	2.4	0.7	4.4	--	--	--
Pyrola secunda	--	0.1	0.05	0.2	--	0.2	--	--	--
Pedicularis lapponica	--	--	--	--	--	--	0.01	0.06	0.2
Pedicularis labradorica	--	--	--	--	--	--	0.01	0.1	--
Pedicularis langsdorfii	--	0.03	0.3	0.02	0.06	0.3	--	--	--
Pedicularis capitata	--	0.06	0.05	1.5	0.6	--	--	--	--
Pedicularis kaneii	0.6	0.02	0.6	--	--	0.01	0.01	--	--
Pinguicula villosa	--	--	--	--	0.01	--	--	0.01	0.05
Petasites frigidus	1.1	0.01	0.7	0.4	--	1.2	--	0.3	--
Senecio atropurpureus	0.2	0.4	0.4	0.4	0.5	1.8	0.05	0.7	0.4
Hierochloe alpina	--	0.8	0.06	--	--	0.3	--	1.0	--
Arctagrostis latifolia	--	0.9	1.1	0.1	0.4	0.8	0.4	0.4	0.1
Poa spp.	0.7	--	--	--	--	0.6	0.7	--	0.6
Eriophorum vaginatum	12.6	9.8	20.9	27.5	39.0	20.5	48.5	34.0	24.5
Kobresia myosuroides	--	--	0.05	--	--	--	--	--	--
Carex bigelowii	16.5	13.2	10.9	8.2	8.2	15.5	10.7	3.5	3.4
Carex rariflora	--	--	--	--	0.07	--	--	--	--
Luzula confusa	--	--	--	--	--	0.1	0.3	0.9	0.4

Plate 4 A Moss-Eriophorum vaginatum stand in a large depression between the outer ridges of the involuted hill.

Table 6. Species cover values for the Lichen-Ledum palustre ct on the involuted hill.

	Polygons			Snow banks	
Stand no.	7	23	30	22	24
$\bar{x}$ cover					
vascular	99.1	131.5	85.3	102.5	137.4
moss	8.5	17.5	11.5	32.5	27.5
lichen	34.5	40.0	23.0	43.0	23.0
No. Vascular species	14	19	12	20	22
Cover Vascular species					
Salix fuscescens	--	0.8	--	--	--
Salix glauca	0.6	0.3	--	3.3	2.6
Salix pulchra	0.05	--	--	--	--
Betula glandulosa	32.0	46.5	18.5	14.0	29.5
Empetrum nigrum	9.2	17.2	3.8	13.0	11.5
Ledum palustre	24.5	26.9	25.0	26.0	28.0
Andromeda polifolia	0.01	--	--	--	--
Arctostaphylos alpina	--	--	4.9	6.6	9.8
Arctostaphylos rubra	0.3	--	2.6	--	--
Vaccinium vitis-idaea	25.0	25.5	18.5	18.0	22.0
Vaccinium uliginosum	--	0.01	--	0.1	--
Stellaria spp.	0.1	0.6	--	--	0.3
Cardamine hyperborea	--	0.1	--	--	--
Rubus chamaemorus	4.2	9.7	9.8	2.5	0.4
Lupinus arcticus	--	0.1	--	0.6	2.6
Pyrola grandiflora	--	--	--	--	2.4
Pyrola secunda	--	--	--	--	0.1
Pedicularis lapponica	--	0.05	--	0.05	0.4
Pedicularis labradorica	--	0.02	--	0.06	--
Pedicularis langsdorfii	0.6	--	--	1.1	0.6
Pedicularis kaneii	--	--	--	0.05	0.07
Petasites frigidus	--	--	--	3.9	9.5
Senecio atropurpureus	0.3	--	--	0.3	0.05
Hierochloe alpina	0.9	1.7	--	0.1	0.05
Arctagrostis latifolia	--	0.02	0.1	1.3	1.4
Poa spp.	--	0.06	0.4	--	0.01
Eriophorum vaginatum	--	0.8	--	4.0	4.0
Carex bigelowii	1.3	1.1	1.0	5.3	11.0
Carex rariflora	--	--	0.3	--	--
Luzula confusa	--	0.02	0.4	2.2	1.1

Plate 5 Well developed high-center polygons occupied by stands of the Lichen-*Ledum palustre* ct. The site is typified by poor drainage and organic soils. In the background there is a stand of *Salix glauca*-*Lupinus arcticus* which is on a better-drained outer ridge.

Plate 6 Snowbank sites on the involuted hill are usually occupied by stands of the Lichen--Ledum palustre ct. The snowbank results in shallow thawed layers and water-logged soils in these stands.

includes stands in snowpack sites (# 22,24) where water from melting snow is trapped in the depressions. Most of the stands of this ct are located in the large depressions between the outer ridges of the hill and beside the large ice-wedges which occur on top of the hill.

Lichens (33%) reach their greatest cover on the hill in this ct. Moss cover is much lower (20%) than in the Moss-*E. vaginatum* ct. *Betula glandulosa* is the dominant vascular plant but its cover (28%) is lower than the mean for the hill and its vigour is poor in comparison to that in the upland cts. In the Lichen-*L. palustre* ct, *B. glandulosa* has a mean height of 7 cm while in the two upland ct's it has a mean height of 25 cm. *Salix glauca* at 1% is at its lowest abundance on the hill. The heaths *Ledum palustre* (26%) and *Arctostaphylos alpina* (4%) are at their highest cover values.

Several species, while not having high cover values, have a much greater abundance in the Lichen - *L. palustre* ct than they do in other community types on the hill. These are: *Carex rariflora*, *Luzula confusa*, *Salix fuscescens*, *Rubus chamaemorus*, *Pedicularis langsdorfii*, and *P. lapponica*.

4.1.4.3 Lotic Wetland Tundra Group

5. *Salix pulchra-Alnus crispa* community type (stands 26,34) (Table 7, Plate 7)

The *Salix pulchra-Alnus crispa* ct is found only along drainage

Table 7. Species cover values for the *Salix pulchra*-*Alnus crispa* ct on the involuted hill.

Stand no.	26	33
$\bar{x}$ cover		
vascular	209.5	199.5
moss	21.7	49.5
lichen	1.1	2.1
No. Vascular species	22	26
Cover Vascular species		
Salix glauca	8.2	1.8
Salix pulchra	52.9	23.7
Betula glandulosa	29.5	37.5
Alnus crispa	3.8	42.4
Empetrum nigrum	6.8	27.0
Ledum palustre	2.4	15.0
Arctostaphylos alpina	--	0.8
Arctostaphylos rubra	2.6	0.3
Vaccinium vitis-idaea	3.6	10.2
Vaccinium uliginosum	13.0	5.0
Equisetum arvense	20.9	0.1
Stellaria spp.	0.05	0.5
Anemone richardsonii	1.1	--
Cardamine bellidifolia	0.5	--
Cardamine hyperborea	--	1.5
Rubus chamaemorus	6.1	2.9
Lupinus arcticus	1.1	1.9
Pyrola grandiflora	8.2	3.3
Pyrola secunda	0.4	0.07
Pedicularis lapponica	--	0.05
Pedicularis capitata	0.4	0.8
Petasites frigidus	17.2	6.1
Senecio atropurpureus	--	0.3
Hierochloe alpina	--	1.8
Arctagrostis latifolia	10.9	5.0
Poa spp.	--	0.05
Eriophorum vaginatum	--	0.8
Carex bigelowii	19.8	10.6
Carex capillaris	0.05	--

Plate 7 A Salix pulchra-Alnus crispa stand in a drainage channel which dissects an outer ridge of the involuted hill. Deciduous shrubs attain their maximum size and vigor along these channels.

channels that cut through the outer ridges of the involuted hill. Snow lies late into the summer in these channels and water was observed flowing through them all summer. Despite the late-lying snow, these habitats support a vigorous shrub community. *Salix pulchra* attains a cover of 38%, *Betula glandulosa* 34% and *Alnus crispa* 23%. Shrubs also reach their maximum height in this ct with *Salix pulchra* growing to 2.2 m and *Betula glandulosa*, *Alnus crispa* and *Salix glauca* being at 1.5 m. In this ct *Salix glauca* has a cover of only 5%.

The only sites on the involuted hill that support *Alnus crispa* are the lower reaches of these drainage channels. While water flows through them all summer, the snow does not linger as long as in the upper reaches. Other vascular plants found only in the *S. pulchra-A. crispa* ct are *Equisetum arvense*, *Ranunculus lapponicus* and *Saussurea angustifolia*. Additionally, *Arctostaphylos rubra*, *Vaccinium uliginosum*, *Anemone richardsonii*, *Cardamine bellidifolia*, *C. hyper-borea*, *Arctagrostis latifolia* and *Carex bigelowii* attain their highest cover values in this ct. *Ledum palustre*, *Vaccinium vitis-idaea* and lichens are at their lowest cover values.

4.2 Soils

4.2.1 Classification

A feature common to all soils on the involuted hill is the presence of permafrost near the ground surface. Thaw depths are no

greater than 60 cm in all ct's. Because the thaw depths extend to less than 1 m, soils on the hill all belong to the Cryosolic order (Canada Soil Survey Committee 1978).

Classification of Cryosols to the great group level is determined by the degree of cryoturbation and the development of organic horizons (Canada Soil Survey Committee 1978). Pettapiece (1975) points out that the formation of earth hummocks and the disruption of soil horizons are the 2 major phenomena associated with cryoturbation in the Low Arctic. Thus the presence or absence of these 2 phenomena is an effective indicator for separating Static and Turbic Cryosols. The third great group, Organic Cryosol, is associated with peat polygon landforms. These soils are defined as having an organic surface horizon of greater than 30% organic matter content which must be greater than 40 cm thick or more than 10 cm thick over an ice layer that is at least 30 cm thick (Canada Soil Survey Committee 1973; Zoltai and Tarnocai 1974).

Earth hummocks and ice wedge polygons are common microrelief features on the hill. Earth hummocks tend to be more prevalent in upland ct's while ice-wedge polygons increase in importance in the depressional communities. In the *S. glauca*-*L. arcticus* ct earth hummocks cover from 30-70% of the land surface with most stands being in the 60-70% range. The *B. glandulosa*-*V. vitis-idaea* ct has an earth hummock cover of 20-70% with the modal cover being 50-60%, slightly less than the *S. glauca*-*L. arcticus* ct. In both ct's inter-hummock hollows occur in the remaining spaces. The earth hummocks range from

5-30 cm in height but most are between 10-15 cm.

Most soils in the upland stands have disrupted or discontinuous horizons, especially at the mineral-organic interface or between mineral horizons. Buried, highly humified, organic horizons are common. Based on the abundant earth hummocks and disrupted horizons it appears that the soils in the upland stands have been strongly affected by cryoturbation. As the upland soils are both cryoturbated and have surface organic horizons less than 40 cm thick they are classified as belonging to the Turbic Cryosol great group.

Earth hummocks are much less common in depressional stands. In the Moss-*E. vaginatum* ct earth hummocks occupy between 5-70% of the ground surface but in most stands only 20-30% of the ground is so covered. Tussocks and hollows cover the remaining ground surface. The hummocks are mostly 10-15 cm in height. Poorly developed ice-wedge polygons are common in this ct. Only 3 soil profiles in this ct (1 in stand 11 and 2 in stand 19) show disrupted horizons; other profiles show little or no breakage of the horizons. Buried organic horizons are not found in any of the profiles. It thus appears that most soils within the Moss-*E. vaginatum* ct have not been strongly affected by cryoturbation. Therefore, soils of this ct are classed as being dominantly Static Cryosols with minor inclusions of Turbic Cryosols in stands 11 and 19.

Earth hummocks are absent from the Lichen-*L. palustre* ct, except in stands 22 and 24. High center polygons account for the microrelief

in the stands. Stands 22 and 24 have a microrelief more similar to upland ct's in that earth hummocks cover 32 and 56% of their ground surfaces respectively.

Soils in the other 3 stands of the Lichen-L. palustre ct have developed on high center polygons. The soils from stand 23, the only site sampled in this ct, all have surface organic horizons with greater than 78% organic matter content; the shallowest depth to an ice-rich organic horizon was 19 cm. The thickness of this icy horizon is not known as it was not possible to dig into it. The other 2 polygonal stands also have well developed peat polygons of the same size. Therefore, these soils belong to the Organic Cryosol great group.

No soil pits were dug in stands 22 and 24 so it is not possible to classify the soils of these stands. However, the presence of earth hummocks would seem to indicate that these stands are underlain by either Turbic or Static Cryosols.

No soil pits were dug in the S. pulchra-A. crispa ct, primarily due to its small areal extent on the involuted hill. It is, therefore, not possible to classify these soils beyond the Cryosolic order.

Soils from 3 Turbic Cryosol subgroups are found in the upland S. glauca-L. arcticus ct: Brunisolic, Orthic, and Gleysolic. The upland B. glandulosa-V. vitis-idaea ct also contains soils of the Brunisolic

Turbic Cryosol and Orthic Turbic Cryosol subgroups. With the exception of the few Gleysolics, soils of the two upland ct's show a distinct horizonation in the mineral part of the solum. The upper mineral horizon is more finely structured and redder in hue than the underlying horizon. These characterisitics define the upper horizon as being a Bm (Canada Soil Survey Committee 1978). In most profiles this horizon is less than 10 cm thick and therefore the soils are Orthic Turbic Cryosols. One pit in stand 8 and 2 in stand 27 had Bm horizons greater than 10 cm thick and are classified as Brunisolic. A gleyed mineral horizon of low chroma was located immediately above or near the frost table in all upland sites but even in the Gleysolic soils no mottling was evident.

A Brunisolic Static Cryosol and an Orthic Static Cryosol were found in the Moss-*E. vaginatum* ct in stands 19 and 29 respectively. However, all other soils in this ct are either Gleysolic Turbic Cryosols or Gleysolic Static Cryosols. With the exception of the Orthic and Brunisolic sites, soils of the depressional Moss-*E. vaginatum* ct differ from the upland stands in 2 major respects. Firstly, the mineral part of the solum consists of a single horizon. The structure of this horizon is uniform throughout the profile but ranges from fine to coarse granular depending on the location of the stand. This horizon has a low chroma (grey), often with red-brown mottling, indicating active gleying processes. This horizon is either Bg or BCg. Secondly, in depressional ct's, earth hummocks are not common, and disrupted, broken or buried horizons are rare; hence, Static Cryosols are common.

Soils of the depressional Lichen-*L. palustre* ct that have developed on high-center polygons belong to either the Mesic Organic Cryosol or Humic Organic Cryosol subgroups. Classification depends upon the degree of humification of the organic layer immediately above the permafrost table. Since sampling of this ct was limited it is not possible to judge the relative importance of these subgroups.

4.2.2 Soil Morphology

Salix glauca-Lupinus arcticus ct

Frost-induced microrelief features are common in the stands of the *S. glauca-L. arcticus* ct. The degree of cryoturbation is outlined in section 4.2.1.

While the mean thickness of organic matter in the hollows (11.3 cm) of this ct is not significantly different from that of the other ct's, that on the earth hummocks (6.3 cm) is significantly less than that found on earth hummocks of the *B. glandulosa-V. vitis-idaea* ct or that on the ridges of the Lichen-*L. palustre* ct (Table 8). Thaw depths under the hummocks in the *S. glauca-L. arcticus* ct extended to a mean of 42.3 cm, the thickest on the hill. However, the mean depth of thaw in depressions of this ct was only 25.3 cm, which is not significantly deeper than that of the other ct's (Table 8).

A surface fibric organic horizon 5-14 cm thick occurred in all soil profiles of this ct. Further, in 8 of the 15 profiles a well

Table 8. Physical characteristics of the soils in the community types on the involuted hill.

Soil Characteristics	Community Types			
	Salix[D]	Betula[E]	Moss[F]	Lichen[G]
Organic matter (%)[AB]				
Organic	57(10.8)a	59(11.4)ab	65(10.7)b	81(3.0)c
Mineral	5(2.6)a	6(2.7)a	7(2.8)a	---
Depth organic matter (cm)				
Hummocks	6.3(4.2)a	13.6(8.6)b	11.1(7.3)ab	22.4(3.3)c
Hollows	11.3(2.5)a	13.0(5.6)a	16.8(4.8)a	---
Thaw depth (cm)				
Hummocks	42.3(7.1)a	34.2(9.9)b	32.4(13.1)bc	22.4(3.3)c
Hollows	25.3(17.6)a	22.6(9.0)a	21.8(4.6)a	---
Sand (%)[BC]	13 (9.5)a	20 (5.2)b	12 (6.4)a	---
Silt (%)	38 (7.3)ab	35 (2.7)a	41 (3.6)b	---
Clay (%)	49 (9.1)a	45 (3.4)a	47 (6.4)a	---

A. Any two means in a row not followed by the same letter are significantly different at 5%. Numbers in brackets are standard deviations.
B. Hummocks and hollows are combined as they are not significantly different at 5%.
C. From mineral horizon only.
D. _S. glauca-L. arcticus_ organic matter, sand:silt:clay % n=10 organic n=13 mineral
organic matter, active layer depths n=11 hummocks n=3 hollows
E. _B. glandulosa-V. vitis-idaea_ organic matter, sand:silt:clay % n=17 organic n=13 mineral
organic matter, active layer depths n=19 hummocks n=10 hollows
F. Moss-_E. vaginatum_ organic matter, sand:silt:clay % n=26 organic n=15 mineral
organic matter, active layer depths n=16 hummocks n=18 hollows
G. Lichen-_L. palustre_ organic matter % n=4
organic, active layer depths n=5

decomposed organic horizon 3-11 cm thick underlies the surface fibric horizon. The average organic matter content of these 2 horizons in the S. glauca-L. arcticus ct was 57%, significantly less than that in depressional ct's, but not significantly different from that in the B. glandulosa-V. vitis-idaea ct.

The mineral portion of the solum in Orthic and Brunisolic Turbic Cryosols consists of 2 horizons: a thin, red-brown, fine granular horizon underlain by a coarse granular grey horizon. The latter horizon extends down to the frost table. The Gleysolic Turbic Cryosols have only a single, coarse granular structured, grey mineral horizon. A well humified organic horizon often separates this horizon from the frost table. The average organic matter content of these mineral horizons is 5%, not significantly different from that of the B. glandulosa-V. vitis-idaea or Moss-E. vaginatum ct's.

The sand:silt:clay ratio of the mineral horizons is 13:38:49; hence the texture is classified as clay (Canada Soil Survey Committee 1978). This ratio is not significantly different from the Moss-E. vaginatum ct (12:41:47) but it has significantly less sand and more silt than is found in the mineral horizons of the B. glandulosa-V. vitis-idaea ct (21:34:45) (Table 8).

Under both hummocks and hollows roots of deciduous shrubs, heaths and herbs frequently extend through the organic horizons into the upper part of the mineral horizon.

Betula glandulosa-Vaccinium vitis-idaea ct

As in the *S. glauca-L. arcticus* ct earth hummocks and disrupted soil horizons are common features in this ct. The extent of cryoturbation is outlined in section 4.2.1.

Mean organic matter thickness in hollows is 13.0 cm, not significantly different from the other ct's. On hummocks organic matter averages 13.6 cm thick, which is not significantly different from the Moss-*E. vaginatum* ct but is significantly thinner than the Lichen-*L. palustre* ct, and significantly thicker than the *S. glauca-L. arcticus* ct (Table 8).

All soil profiles in this ct have a well developed fibric organic horizon at the ground surface. Under the hummocks this horizon ranges from 1-12 cm thick ($\bar{x}$ = 6.8) while in the hollows it is from 2-17 cm thick ($\bar{x}$ = 8.2). In all but 4 of the 30 soil pits a humic organic horizon underlies the fibric horizon. Its thickness ranges from 2-25 cm ($\bar{x}$ = 6.8) under the hummocks and 2-11 cm ($\bar{x}$ = 4.9) in the hollows. There is no significant difference in the depths of any of these horizons. The average organic matter content of these horizons is 59%, significantly less than those of the Lichen-*L. palustre* or Moss-*E. vaginatum* ct's (Table 8).

The mean thickness of the active layer in the hollows of this ct is 22.6 cm, not significantly different from those of the other ct's (Table 8). Under hummocks the thaw layer thickens to a mean of

34.2 cm, which is significantly thinner than that of the *S. glauca-L. arcticus* ct, significantly thicker than that of the Lichen-*L. palustre* ct, and not significantly different from that of the Moss-*E. vaginatum* ct (Table 8).

The mineral part of the solum shows well developed horizonation. The upper mineral horizon is 4-16 cm thick, with a fine granular structure and red-brown color. Its lower boundary is often markedly disrupted. A coarse, granular structured mineral horizon of grey to dark grey color underlies the fine structured horizon and extends down to the permafrost table. The average organic matter content of these horizons is 6.5%, not significantly different from those of the other ct's (Table 8). As stated in 4.1.2, these horizons had significantly more sand than did the mineral horizons in other ct's. However, the texture of these soils is still classified as clay (Canada Soil Survey Committee, 1978).

The roots of deciduous shrubs, heaths and herbs extend through the organic horizons; some were found in the upper portion of the fine granular structured mineral horizon.

Moss-*Eriophorum vaginatum* ct

The microrelief of the Moss-*E. vaginatum* ct is distinctly different from those of both the upland ct's and the other depressional ct's. It differs from upland ct's in that earth hummocks cover only about 35% of the land surface, *Eriophorum* tussocks cover about

25% and hollows cover the remaining 40%. Peat polygons, so characteristic of the Lichen-*L. palustre* ct, are either poorly developed or absent in the Moss-*E. vaginatum* stands. Disrupted soil horizons are rare, even under earth hummocks, and buried organic horizons are absent from all soil profiles in this ct.

The active layer beneath the hollows of this ct has a mean thickness of 21.8 cm, not significantly different from those of the other ct's (Table 8). Under hummmocks the mean thickness of the thaw layer is 32.4 cm, significantly thinner than those of the *S. glauca-L. arcticus* ct.

The thickness of the organic matter in both hummocks ($\bar{x}$ = 11.1 cm) and hollows ($\bar{x}$ = 16.8 cm) is not significantly different from those of the same micro-sites in the *S. glauca-L. arcticus* and *B. glandulosa-V. vitis-idaea* ct's. However, in contrast to the upland ct's, the thaw layer in many hollows of the Moss-*E. vaginatum* ct consists entirely of organic material. Under these conditions roots are not able to contact the mineral horizon. While there is still a thin fibric organic horizon at the surface of these soils, mesic organic horizons predominate instead of the humic horizons found in upland stands. The average organic matter content of these horizons is 65%, significantly higher than those of the *S. glauca-L. arcticus* ct, significantly less than the Lichen-*L. palustre* ct and shows no significant difference from those of the *B. glandulosa-V. vitis-idaea* ct.

Horizonation of the mineral part of the solum is almost entirely

absent in the Moss-E. vaginatum ct. A single, red-brown mottled, grey horizon of granular structure extends to the base of the thaw layer. The average organic matter content of the mineral horizons is 67%, not significantly different from those of the other ct's (Table 8). The sand:silt:clay ratio is not significantly different from that of the S. glauca-L. arcticus ct and the texture is again defined as clay. Less sand and more silt are found in these mineral horizons than in those of the B. glandulosa-V. vitis-idaea ct.

With the exception of Eriophorum vaginatum, roots are restricted to the top few centimeters in the organic part of the solum in the Moss-E. vaginatum ct. The roots of E. vaginatum were observed to extend into the mineral part of the solum.

Lichen-Ledum palustre ct

On the open, west-facing slope of the hill (stand 22) earth hummocks cover 32% of the land surface. In the more enclosed, north-facing slope (stand 24) the hummmocks cover significantly more area, 56%. No pits were dug in these 2 stands so it is not possible to describe their soil profiles. However, thaw depths were measured when the vegetation was surveyed in mid-July. Under hummocks the thawed layer was 37 cm thick in stand 22 and 45 cm thick in stand 24; under hollows the thawed layer was 19 and 21 cm thick respectively.

In all 5 soil pits dug in stand 23 the thawed layer was restricted to the organic part of the solum; no mineral horizons appeared in any

of the examined profiles. Mean thaw depths were 22.4 cm, significantly thinner than that found under hummocks in either of the upland ct's, but not significantly thinner than that of the Moss-_E. vaginatum_ ct, and not significantly different from those beneath hollows of the other ct's (Table 8).

Organic matter above the frost table also had a mean thickness of 22.4 cm in the high-center polygonal stand, significantly thicker than those in all other ct's under either hummocks or hollows (Table 8).

Four of the 5 pits had a fibric organic surface horizon varying between 12-14 cm in thickness. In 3 of the 4 pits there was a mesic horizon 5-6 cm thick beneath the fibric surface horizon. This mesic horizon was basal in 1 of the 3 pits but in the other 2 pits a humic horizon 7-9 cm thick occurred above the frost table. The fifth pit had a 21 cm deep humic horizon under a 2 cm thick surface fibric layer. At the bottom of this pit there was a 2 cm thick mesic horizon above the frost table.

Roots are abundant in the upper fibric horizon but did not penetrate into the lower organic horizons.

4.2.3 Soil Moisture

The two upland ct's, _S. glauca-L. arcticus_ and _B. glandulosa-V. vitis-idaea_, have mean soil moisture contents of 215 and 256% respectively, in the organic horizons of their hummocks, and 247 and

286% in the organic horizons of their hollows. There are, however, no significant differences in soil moisture content between these two ct's in either hummocks or hollows. Nor are there significant differences in soil moisture content between hummocks and hollows within either ct (Table 9).

The depressional Moss-E. vaginatum and Lichen-L. palustre ct's both have significantly higher soil moisture contents in their organic horizons than do the upland ct's. In the Moss-E. vaginatum ct organic horizons of hummocks have a mean soil moisture content of 494% while those of hollows have a mean of 630%. These values are significantly higher than those of the upland ct's but are not significantly different from those of the Lichen-L. palustre ct which has a mean soil moisture content of 542% (Table 9). Thus soil moisture content in the organic horizons clearly separates upland and depressional ct's. While soil moisture measurements were not made in the 2 snowbank stands (22 and 24), the extremely wet conditions of these stands can easily be inferred from the presence of standing water at the soil surface until late June. It seems very likely, therefore, that these 2 stands have soil moisture contents similar to the other depressional stands. Similar inferences can be made about the S. pulchra-A. crispa ct. Again no soil samples were collected but surface water flowed through these stands all summer, indicating extremely wet soil conditions.

Soil moisture content in the mineral horizons does not show as clear a pattern as the organic horizons. Mean mineral soil moisture

Table 9. Soil moisture content and excess soil moisture in the community types on the involuted hill.

Soil Moisture	Community Types			
	Salix[C]	Betula[D]	Moss[E]	Lichen[F]
Content (%)				
Organic, Hummocks[A]	215(74.3)a	256(76.4)a	494(177.0)b	542(85.3)b
Organic, Hollows	247(30.2)a	286(107.6)a	630(201.5)b	---
Mineral[B]	28(9.4)ab	26(6.5)a	35(10.3)b	---
Excess (%)				
Organic, Hummocks	76(51.2)a	103(47.0)a	354(177.4)b	354(232.9)b
Organic, Hollows	101(26.1)a	137(75.0)a	444(185.6)b	---
Mineral[B]	-3.3(4.5)a	-4.0(3.4)a	-2.7(4.1)a	---

A. Any two means in a row not followed by the same letter are significantly different at 5%. Numbers in brackets are standard deviations.

B. Hummocks and hollows are combined as they are not significantly different at 5%.

C. *S. glauca-L. arcticus* n=6 organic hummock n=4 organic hollow n=13 mineral

D. *B. glandulosa-V. vitis-idaea* n=12 organic hummock n=5 organic hollow n=13 mineral

E. Moss-*E. vaginatum* n=9 organic hummock n=13 organic hollow n=15 mineral

F. Lichen-*L. palustre* n=4 organic hummock

content is significantly lower in the B. glandulosa-V. vitis-idaea ct (26%) than in the Moss-E. vaginatum ct (35%), but mineral soil moisture in the former ct does not differ significantly from that in the S. glauca-L. arcticus ct (28%). There is also no significant difference in mineral soil moisture content between the S. glauca-L. arcticus ct and the Moss-E. vaginatum ct (Table 9). The slightly drier conditions of the B. glandulosa-V. vitis-idaea ct may be due to its sandier soil texture.

'Excess soil moisture,' defined as the difference between the soil moisture content and the water retention at -1/3 bar, shows a pattern similar to soil moisture content. Again the 2 upland cts have drier soil conditions; excess water in the organic horizons on hummocks is 76% in the S. glauca-L. arcticus ct and 103% in the B. glandulosa-V. vitis-idaea ct. Organic matter in hollows of the 2 ct's have mean excess soil moistures of 101% and 137% respectively. There is no significant difference in excess soil moisture content between the 2 ct's; nor is there a significant difference in excess soil moisture content between hummocks and hollows within either ct (Table 9).

The Moss-E. vaginatum and Lichen-L. palustre ct's both have significantly higher excess soil moisture content than the upland ct's. There is no signficant difference in excess soil moisture between the 2 depressional ct's. In the Moss-E. vaginatum ct mean excess soil moisture is 354% in organic horizons on hummocks and 444% in hollows. The high-center polygon stand of the Lichen-L. palustre ct has a mean excess soil moisture of 354%, identical to that of the

organic horizon on hummocks in the Moss-E. vaginatum ct (Table 9).

Excess soil moisture of the organic horizons, like soil moisture content, appears to be an effective variable for separating upland from depressional ct's.

Slight soil moisture deficits occur in the mineral horizons of the 3 ct's which have these horizons in the active layer of the solum. The S. glauca-L. arcticus ct has a mean soil moisture deficit of -3.3%, the B. glandulosa-V. vitis-idaea ct -4% and the Moss-E. vaginatum ct -2.7%. There is no significant difference between the soil moisture deficits of these three ct's (Table 9).

4.2.4 Soil Nutrients and pH

There have been several reports citing the low availability of mineral nutrients in arctic environments. (Warren-Wilson 1954, Hielman 1966, 1968, Haag 1974, Everett 1980) However, there are but a few papers that discuss variations in nutrient availability among ct's within a given area (cf. Webber 1978). Several significant variations in soil nutrients were found on the involuted hill. Generally, the depressional ct's have lower available nutrient concentrations than the upland ct's. This trend is especially evident in organic horizons; mineral horizons are less variable.

Organic Horizons

The *S. glauca-L. arcticus* ct has significantly higher total nitrogen ($\bar{x}$ = 0.68 %) than the other ct's. The *B. glandulosa-V. vitis-idaea* ct is second highest, with a mean nitrogen content of 0.58 ppm; this ct's concentration was significantly higher than either of the depression ct's (Table 10).

The highest concentration of phosphorus in organic horizons is again found in the *S. glauca-L. arcticus* ct ($\bar{x}$ = 2.52 ppm). Significantly lower concentrations are found in the *B. glandulosa-V. vitis idaea* and Moss-E. *vaginatum* ct's (1.37 and 1.35 ppm, respectively), but the *B. glandulosa-V. vitis-idaea* ct has a higher concentration than the Lichen-*L. palustre* ct (Table 10).

The Lichen-*L. palustre* ct has a significantly lower concentration of available potasium (0.14 me/100 g) than the other ct's, which have concentrations ranging from 0.42 to 0.49 me/100 g (Table 10).

Available calcium concentrations differ greatly between upland and depressional ct's. The *S. glauca-L. arcticus* and *B. glandulosa-V. vitis-idaea* ct's have similar concentrations, 15.4 and 13.3 me/100 g, and both are significantly higher than those of either depressional ct. The Moss-*E. vaginatum* and Lichen-*L. palustre* ct's also have similar concentrations, 8.0 and 7.3 me/100 g, respectively (Table 9).

While there is no significant difference in available magnesium

Table 10. Macro nutrients, cation exchange capacity, and pH of the soils in the community types on the involuted hill.

Soil Nutrients*	Community Types			
	Salix[I]	Betula[I]	Moss[K]	Lichen[L]
Total N (%)[A]				
Organic	0.68(0.12)a*	0.58(0.08)b	0.41(0.16)c	0.43(0.12)c
Mineral	0.24(0.09)a	0.27(0.08)a	0.25(0.07)a	---
Total P (%)[B]				
Organic	2.52(1.17)a	1.37(0.86)b	1.35(1.23)cb	0.53(0.40)c
Mineral	0.53(0.47)a	0.49(0.43)a	0.36(0.26)a	---
Available K (m.eg./100 gm)[C]				
Organic	0.49(0.16)a	0.43(0.22)a	0.42(0.14)a	0.14(0.09)b
Mineral	0.40(0.16)a	0.35(0.13)a	0.30(0.08)b	---
Available Ca (m.eg./100 gm)[D]				
Organic	15.43(3.69)a	13.31(5.36)a	8.04(4.39)b	7.28(3.10)b
Mineral	12.48(4.51)a	9.84(4.04)ab	7.80(4.51)b	---
Available Mg (m.eg./100 gm)[E]				
Organic	5.11(2.02)a	3.90(1.63)ab	3.45(1.09)b	2.66(1.43)b
Mineral	5.12(0.88)a	5.01(0.95)a	5.38(2.65)a	---
Available Na (m.eg./100 gm)[F]				
Organic	0.23(0.23)a	0.24(0.11)a	0.24(0.06)ab	0.34(0.14)b
Mineral	0.30(0.26)a	0.24(0.06)a	0.40(0.57)a	---
C.E.C. (m.eg./100 gm)[G]				
Organic	41.24(5.38)a	38.04(7.84)a	30.35(8.44)b	26.07(8.40)b
Mineral	30.71(7.81)a	31.38(4.12)a	30.81(5.54)a	---
pH[H]				
Organic	5.2(5.2)a	5.4(5.9)a	5.1(5.2)a	4.4(4.2)a
Mineral	6.5(6.9)a	5.0(5.2)a	4.9(5.0)a	---

* Any two means in a row not followed by the same letter are significantly different at 5%. Numbers in brackets are standard deviations.

A micro-kjeldahl nitrogen

B NaOH fusion

C NH_4 acetate soluble potassium

D NH_4 acetate soluble calcium

E NH_4 acetate soluble magnesium

F NH_4 acetate soluble sodium

G NH_4 acetate cation exchange

H $CaCl_2$

I S. glauca-L. arcticus n=10 organic n=13 mineral

J B. glandulosa-V. vitis-idaea n=17 organic n=13 mineral

K Moss-E. vaginatum n=26 organic n=15 mineral

L Lichen-L. palustre n=4 organic

concentrations between the 2 upland ct's, the *B. glandulosa-V. vitis-idaea* ct has a slightly lower concentration. The upland *S. glauca-L. arcticus* ct has a significantly higher available magnesium concentration than the 2 depressional ct's (Table 10).

Sodium content shows a reversal in the general trend; the 2 depressional ct's have significantly higher sodium concentrations than the upland *S. glauca-L. arcticus* ct. However, there is no significant difference in sodium concentration between the *B. glandulosa-V. vitis-idaea* and Moss-*E. vaginatum* ct's.

The cation exchange capacity (CEC) of the organic horizons shows a clear separation between upland and depressional ct's. The upland *S. glauca-L. arcticus* and *B. glandulosa-V. vitis-idaea* ct's have similar capacities, 41.2 me/100 g and 38.0 me/100 g respectively. Both of these capacities are significantly greater than those of either the Moss-*E. vaginatum* ct (30.4 me/100 g) or the Lichen-*L. palustre* ct (26.1 me/100 g) (Table 10). There is no significant difference in CEC between the latter ct's.

To summarize, there appears to be a gradient of nutrient availability from lowest values in organic horizons of the Lichen-*L. palustre* ct and increasing amounts through the Moss-*E. vaginatum* ct and *B. glandulosa-V. vitis-idaea* ct, to the maximum concentrations in the *S. glauca-L. arcticus* ct.

Mineral Horizons

Trends in nutrient concentrations are not as evident in the mineral portion of the solum as they are in the organic portion. Most of the macronutrients (nitrogen, phosphorus, magnesium and sodium) and the CEC show no significant differences in concentration amongst the S. glauca-L. arcticus, B. glandulosa-V. vitis-idaea and Moss-E. vaginatum ct's. There is no significant difference in potassium concentrations between the upland S. glauca-L. arcticus (0.40 me/100 g) and B. glandulosa-V. vitis-idaea (0.35 me/100 g) ct's. However, both of the upland ct's have higher concentrations of potassium than the depressional Moss-E. vaginatum ct (0.30 me/100 g). The B. glandulosa-V. vitis-idaea ct has calcium concentrations intermediate between and not significantly different from the S. glauca-L. arcticus ct and Moss-E. vaginatum ct. Calcium concentration is significantly lower in the Moss-E. vaginatum ct than in the S. glauca-L. arcticus ct.

pH

The organic horizons of the upland ct's have a mean pH of 5.2 in the S. glauca-L. arcticus ct and 5.4 in the B. glandulosa-V. vitis-idaea ct. In depressional ct's the average pH of these horizons is 5.1 in the Moss-E. vaginatum ct and 4.2 in the Lichen-L. palustre ct. Although the pH of the organic horizons appears to be slightly lower in depressional ct's there is no significant difference amongst the ct's.

The mineral horizons also gave no evidence of changes in pH amongst the ct's. The mean pH of these horizons in the *S. glauca*-*L. arcticus* ct was 6.5 which was not significantly higher than that of the *B. glandulosa*-*V. vitis-idaea* ct (5.0) or the Moss-*E. vaginatum* ct (4.9).

5.0 DISCUSSION

5.1 Comparison with Tundra Communities and Habitats of Other Arctic Sites

Previous ecological studies make possible a comparison of the ct's found on the involuted hill with those found in other parts of Arctic North America. Such a comparison is made below, based on similarities and differences in species composition, physiognomy and habitat.

The first comparison is with an extensive analysis of arctic plant communities on the eastern Mackenzie Delta by Corns (1974).

Both the *Salix glauca-Lupinus arcticus* and *Betula glandulosa-Vaccinium vitis-idaea* ct's belong to Corns' Low Shrub-Heath type. This classification is based on both ct's being dominated by shrubs of less than 1 m in height, with an understory of heaths and herbs, and the absence of *Alnus crispa*. Corns reports that this type is dominated by *Betula nana*, *Salix glauca*, and *S. pulchra*; it has high cover values for *Empetrum nigrum*, *Vaccinium vitis-idaea*, *Lupinus arcticus* and *Pyrola grandiflora.* Except for the abundance of *S. pulchra* this closely matches the physiognomy and species structure of the upland ct's on the involuted hill.

The Low Shrub-Heath type is "characteristic of the hilltops" (Corns 1974) and frost boils (earth hummocks) are common in it. Thus the habitat of the upland tundra ct's on the involuted hill appears

typical for that of the rest of the Pleistocene Mackenzie Delta. Corns reports that this type is relatively dry and attributes this dryness to removal by wind of snow from these elevated sites. The Low Shrub-Heath type is the most extensive type on the Pleistocene delta covering from 30-70% of the landscape (Corns 1974).

At a lower level of classification, the S. glauca-L. arcticus ct matches Corns' description of the Willow-Heath subgroup. Both the ct and the subgroup can be described as having Salix dominant over Betula with an abundance of both E. nigrum and V. vitis-idaea. The syntaxonomic affinities of the B. glandulosa-V. vitis-idaea ct are not as clear; it may belong to either the Birch-Heath or Birch-Willow-Heath subgroups. Salix cover in the ct is about 29%, Betula 48% and it is not apparent from Corns' description if this cover of Salix is high enough to classify the ct as Birch-Willow-Heath. However, Arctostaphylos rubra and Vaccinium uliginosum, which are reported to be common in both subgroups, are particularly abundant in the Birch-Willow-Heath subgroup. These two species are not common in the B. glandulosa-V. vitis-idaea ct and, therefore, it appears that this ct is most similar to the Birch-Heath subgroup.

The Moss-Eriophorum vaginatum and Lichen-Ledum palustre ct's are classified as belonging to the Herb-Low Shrub-Heath type of Corns (1974). This type is found in low topographic positions and has an abundance of herbs and heaths.

The Moss-E. vaginatum ct can be considered equivalent to the

Sedge-Cottongrass-Heath subgroup of Corns (1974). Both the ct and the subgroup have high covers of *E. vaginatum* and mosses; *Carex bigelowii* is an important member of the community. The Sedge-Cottongrass-Heath subgroup and the closely related Sedge-Heath subgroup are reported to cover between 1 and 10% of the Tuktoyaktuk Peninsula (Corns 1974).

The Lichen-*L. palustre* ct has as its counterpart Corns' (1974) Raised-Center Polygon subgroup. Both the ct and subgroup occur on well developed, high-center polygons with large areas of exposed peat and high covers of *B. glandulosa*, *Rubus chamaemorus*, *L. palustre* and *V. vitis-idaea*. However, Corns (1974) reports that moss cover is low and lichen cover is variable. On the involuted hill moss cover in the Lichen-*L. palustre* ct was only slightly below its mean for the entire hill, and lichen cover was consistently high (though it did vary from 23-43%). This subgroup is reported to cover 4-15% of the Peninsula (Corns 1974).

Finally, the *Salix pulchra*-*Alnus crispa* ct most resembles Corns' (1974) Medium Shrub-Heath type. In both syntaxa shrubs are dense but most are less than 1.5 m tall; *A. crispa*, forbs and/or graminoids are abundant. Both units occur in a late snow-melt area. Corns (1974) states that there is downslope flow of soil water in this type; this situation was also observed on the involuted hill. However, the Medium Shrub-Heath type has high covers of *L. palustre*, *V. vitis-idaea*, *E. vaginatum* and *S. glauca*; these species had low cover values in the *S. pulchra*-*A. crispa* ct. On the Tuktoyaktuk Peninsula this type covered 4-8% of the landscape (Corns 1974).

The Point Barrow I.B.P. site is located on the low lying coastal plain of northern Alaska. Ice-wedge polygons are the only significant elements of relief (Webber 1978). Webber's (1978) Wet *Dupontia fisheri*-*Eriophorum angustifolium* Meadow is found on flat wet sites and polygon troughs. It appears to be ecologically equivalent to the Moss-*E. vaginatum* ct of the involuted hill in terms of habitat and general physiognomy. The species correspondence is not good as *Dupontia fisheri* is absent in the involuted hill ct and the cotton-grass tussock sedge *E. vaginatum* replaces *E. angustifolium*.

The Lichen-*L. palustre* ct has its closest affinity with Webber's (1978) Dry *Luzula confusa* Heath. Both communities are found on high-center polygons and lichens are abundant. Again, however there are some significant differences between the communities. On the involuted hill *L. confusa* reaches its maximum cover value (1%) in this ct but it is much lower in cover than either the heath species or lichens. Webber (1978) describes the characteristic growth-forms as caespitose monocots and fruticose lichens, while on the involuted hill the growth-forms in this ct are dominantly evergreen shrubs and lichens.

Due to the low, flat relief at Barrow there are no communities there that correspond to the upland group found on the involuted hill. The *S. pulchra*-*A. crispa* ct is also missing at Barrow.

At Cape Thompson on western, coastal Alaska, upland sites are better drained with coarser-textured soils (Holowaychuk et al. 1966)

than similar sites on the involuted hill. There is little similarity between the communities on upland sites at Cape Thompson, which are dominated by Dryas-heaths, and those on upland sites on the involuted hill, which are dominated by Salix and Betula shrubs.

High-center polygons at Cape Thompson appear to be drier and the mineral part of the solum is within the active layer. Salix spp., heaths and Carex bigelowii dominate these sites. Similar habitats on the involuted hill are dominated by lichens and L. palustre.

However, the most common community in the Cape Thompson area, the Eriophorum tussock community, is very simiar to the Moss-E. vaginatum ct of the involuted hill. Both ct's occupy low-lying, poorly drained sites, have gleysolic soils, and are dominated by E. vaginatum. Additionally, Ledum palustre, Betula glandulosa and Vaccinium vitis-idaea, which are reported to be common in this community in Cape Thompson, all have cover values of greater than 10% on the involuted hill. It appears that these two ct's are virtually identical.

The Umiat region of Alaska is located within the Foothills Province where the topography is dominated by gently rolling hills (Churchill 1955). Shrub-dominated plant communities are more common at Umiat than on the Arctic Coastal Plain and they show a greater similarity to ct's of the Upland Group on the involuted hill.

Churchill's (1955) Dwarf Shrub-Heath type appears to be ecologically equivalent to the B. glandulosa-V. vitis-idaea ct. Both

ct's are found on upland sites, with _B. glandulosa_, _V. vitis-idaea_, _L. palustre_ and _E. nigrum_ being prominent vascular plants. The stature of the shrubs may be somewhat lower at Umiat than on the involuted hill. The Moss-_E. vaginatum_ ct has a counterpart in Churchill's _Eriophorum_-Dwarf Shrub Heath group of the preceding type. It appears that there is a greater habitat overlap of _Betula_ and _Eriophorum_ at Umiat than on the involuted hill, perhaps reflecting moister conditions at Umiat.

A _Salix glauca_ type is reported for Umiat by Churchill (1955) but unlike the habitat on the involuted hill this type was found in a wet drainage channel with _Sphagnum_ mosses. It does not appear to correspond to the _S. glauca_-_L. arcticus_ ct of the involuted hill except in terms of dominance by _S. glauca_.

An _Alnus crispa_ type at Umiat has close affinities with the _S. pulchra_-_A. crispa_ ct. Both ct's are found in draws with flowing water and are dominated by medium shrubs. _Alnus crispa_ and _S. pulchra_ are the dominant species with _Arctagrostis latifolia_ and _Equisetum arvense_ being common herbs. Mosses are common but lichens have low cover value.

Bliss (1977) states that the ct's found in Truelove Lowland, Devon Island, are closely related to those of the Low Arctic sites found in northern Alaska and the Mackenzie Delta. Comparing the ct's found on the involuted hill to those of Truelove Lowland, however, there appears to be little correspondence.

None of the Upland Group ct's of the involuted hill seem to occur in the Truelove Lowland area (cf. Muc 1977). Upland sites at Truelove are dominated instead by cushion plants with some dwarf shrubs such as *Salix arctica*. By contrast, upland sites on the involuted hill are dominated by low shrubs, herbaceous dicots and ericads.

The only moderately similar communities in the two areas appear to be Muc's (1977) Sedge-Moss type and the Moss-*E. vaginatum* ct. These types are similar in that they occupy low-lying habitats, are dominated by mosses and graminoids, and lichens are rare in them. But there are some significant differences in terms of species composition: *E. vaginatum* replaces *E. angustifolium* and *E. triste*. Also, *Carex bigelowii*, the most common *Carex* in the involuted hill ct, appears to be absent at Truelove Lowland (Muc 1977, Hultén 1968).

From the preceding comparisons it is clear that all the ct's found on the involuted hill have been reported from other regions of Arctic North America. What is exceptional about the hill is that within a small area there are ct's that have been reported from both the Arctic Coastal Plain and the Foothills provinces. Other than the Mackenzie Delta, most areas of coastal lowland tundra in western North America are dominated by communities similar to the Moss-*E. vaginatum* ct or the Lichen-*L. palustre* ct, with shrub-dominated ct's rare or absent.

The prevalence of shrub-dominated ct's on the involuted hill gives it a physiognomy found in more inland and/or upland sites such as the foothills at Umiat. The higher relative relief and wrinkled landscape

of the involuted hill resembles the rolling topography of the foothills province of northern Alaska on a smaller scale, thereby offering suitable habitats for 'foothills' ct's. It thus appears that the uplands of the involuted hills act as disjunct foothill elements.

The Moss-*E. vaginatum* ct, dominant in the depressions of the involuted hill, seems to be common throughout the west coast of Arctic North America (Britton 1966; Wein & Bliss 1974). However, in most other study areas *E. angustifolium* is dominant rather than *E. vaginatum*.

5.2 Vegetation patterns

The distribution of tundra plant communities on an arctic landscape is controlled by a complex of environmental factors and their gradients over space. In the arctic, small changes in relief produce steep environmental gradients thereby creating discrete plant community types (Bliss 1971).

Vegetation on the involuted hill consistently reflects the wrinkled appearance of the landscape. In terms of physiognomy, upland sites are dominated by deciduous shrubs and forbs, while depressional sites are dominated by mosses, lichens and graminoids. Several large ice-wedges occur on the involuted hill. The shoulders of these ice-wedges create habitats similar to upland sites, probably through better drainage. Plant communities on these ice-wedges are vegetatively similar to upland sites and are included in the Upland

Group.

Corns (1974) substantiates this vegetation pattern interpretation for other areas on the Pleistocene Mackenzie Delta. Similarly, both Webber (1978) and Murray (1978) report that plant community types at Barrow are correlated with periglacial geomorphic features. Webber (1978) further postulates that microrelief is the principal control on the plant environment; through its effect on drainage and other substrate relations it determines the distribution of plant species.

5.3 Uniform Factors Among the Community Types

Several environmental parameters show no significant variation between the ct's on the involuted hill. These include organic matter depth in hollows between earth hummocks, active layer thickness in these hollows, soil pH and nitrogen, phosphorus, magnesium, sodium and C.E.C. in the mineral part of the soil profiles. Due to their uniformity among ct's it is assumed that these parameters will not have an influence on vegetation distribution.

It is believed that the involuted hill, despite having several geomorphological features, has had a uniform geological history. That is, the mineral part of the solum is derived from a till (Rampton and MacKay 1971) that was laid down during a single geological period and that the entire hill has been exposed to the same climatic conditions throughout the Quaternary. The uniformity of nutrients in the mineral part of the solum is probably due to a uniform geological history for

the entire hill.

It was previously noted (4.1.4.1) that in the upland sites most mosses were located in the hollows between the earth hummocks. These hollows in effect support patches of the Moss-*E. vaginatum* ct. The mosses contribute to an accumulation of organic matter in the hollows creating conditions similar to those of the Moss-*E. vaginatum* ct. Organic matter has a strong influence on the thermal budget of sites due to its insulative properties (Brown 1973). The relatively deep organic matter of the upland hollows probably retards heat exchange to the ground thereby producing shallow active layers similar in depth to those of the Moss-*E. vaginatum* ct.

5.4 Soil Moisture

Soil moisture content is an environmental parameter which, on the involuted hill, varies significantly between upland and depressional sites. Previous research has done much to substantiate the importance of soil moisture in controlling environmental and vegetation gradients in the arctic (Tedrow and Cantlon 1958, Billings and Mooney 1968, Bliss 1971, Janz 1974). The factor primarily responsible for differences in soil moisture over a given tundra area is relief (Webber 1978); upland sites have better drainage than depressions. Furthermore, wind often removes snow from the higher topographic positions (Corns 1974, Webber 1978). The combination of better drainage and reduced moisture from snow melt results in relatively dry conditions in upland sites on the involuted hill. This observation is

substantiated by Corns' (1974) work in which he reports minimal snow accumulation and drier habitats in the upland Low Shrub-Heath type. Depressional sites which have poorer drainage and greater snow accumulation have significantly higher moisture contents. Soil moisture, with organic matter and thaw depths forms an environmental 'complex-gradient' (*sensu* Whittaker 1975) or soil catena (Figure 5) which may, in turn, control nutrient availability between topographic sites and, by extension, the distribution of ct's (Janz 1974). Soil moisture contents of ct's are described in Table 9.

Depressional stands are characterized by high soil moisture contents with very slowly flowing or stagnant water. The *S. pulchra*-*A. crispa* ct is exceptional in that water flowed through its stands all summer. Thaw depths are shallow in depressional stands, further inhibiting drainage. The lack of free drainage produces anaerobic conditions through a reduction in gas exchange. Evidence for the low amounts of oxygen in these soils is seen in the almost universally mottled appearance of the mineral portion of the solum. Anaerobic decomposition occurs to a greater extent than in more freely drained sites and toxic byproducts such as H_2S often accumulate in the soil (Alexander 1961). Plants occupying these poorly aerated sites have two basic strategies to avoid the oxygen deficiency of the solum.

Firstly, some species have evolved a mechanism whereby oxygen taken in by the shoots is translocated *via* aerenchyma tissues to the roots. Armstrong and Boatman (1967) demonstrated this ability for several species growing in boggy soils with poor aeration. *Eriophorum*

angustifolium under reducing conditions showed iron oxidation around the root tips and it was concluded that oxygen translocation was occurring from the above-ground portion of the plant (Armstrong and Boatman 1967). Further, Stuart and Miller (1982), from work in northern Alaska, found higher levels of oxygen under vehicle tracks occupied by *Eriophorum vaginatum* than in tracks where this species did not occur. They concluded that *E. vaginatum* played a role in aerating very wet tundra soils. On the involuted hill reddish stains were observed around the roots of *E. vaginatum*, providing indirect evidence of iron oxidation and, by extension, oxygen translocation to its roots. Janz (1974) made similar observations about this species. By avoiding the necessity of physically driven soil aeration *E. vaginatum* is able to extend its roots through the water-saturated organic horizon into the more nutrient-rich mineral horizon. This is a mechanism which allows *E. vaginatum* to dominate in depressional sites where the mineral horizon is included in the thawed layer. *Carex bigelowii* is another deep-rooting sedge that reaches its maximum abundance in the Moss-*E. vaginatum* ct. This species may have similar adaptations to the anaerobic conditions.

The *S. pulchra*-*A. crispa* ct had water flowing through it all summer, yet had the best developed shrub cover on the hill. From this observation it is postulated that water itself is not the factor limiting shrub growth but rather the presence or absence of oxygenated water. Water in the stands was constantly flowing and thus likely had more oxygen than other depressional sites. Furthermore, it is expected that flowing water will transport nutrients into and toxins

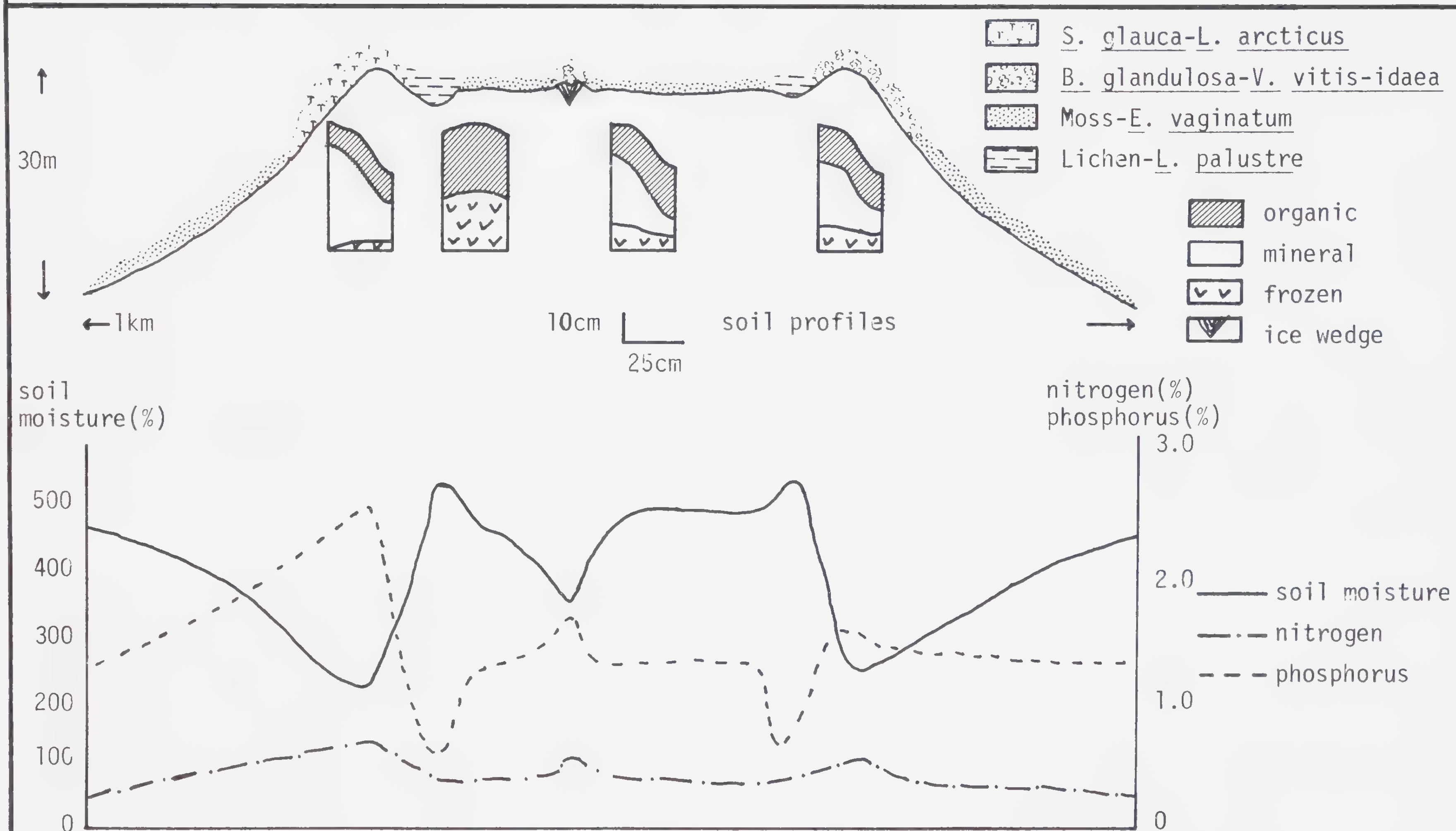


Figure 5. Schematic cross-section of the involuted hill showing locations of the community types; their soil profiles; and their organic horizon moisture, nitrogen, and phosphorus contents.

away from the site.

The second strategy is exhibited by species that Shaver and Cutler (1979) have termed "floaters". These species include heaths and, in some cases, Betula glandulosa. The strategy of these plants is to avoid the wet conditions of the habitat by concentrating most of their root systems within the drier top few centimeters of the surface organic horizon. This shallow rooting strategy was originally discussed by Dennis and Johnson (1970) as a mechanism whereby plants avoid the cold conditions created by the near-surface permafrost horizon. However, as Janz (1974) points out, surficial rooting may also be a response to anaerobic soil conditions. Evidence that some species are using the floater strategy on the involuted hill is seen in both Betula glandulosa and Ledum palustre rooting only in the top few centimeters of the organic horizon in both the Moss-E. vaginatum ct and the Lichen-L. palustre ct. A major ecological problem with this strategy is that the plants are cut off from the relatively nutrient-rich mineral horizon (they may also be vulnerable to intermittent droughts). This partially explains the stunted growth-form shown by B. glandulosa in the Lichen-L. palustre ct. Heaths successfully employ the floater strategy to occupy these marginal habitats because they appear to have developed an effective nutrient storage system (Hadley and Bliss 1964). This system is discussed in more detail below (5.5).

Upland tundra sites are typified by having better drainage and drier soil conditions than depressional sites. Drainage in the

uplands is enhanced by their high topographic positions and relatively thick thawed layers (Figure 5). The more aerated upland soils do not produce the gas exchange and toxicity problems encountered in the depressional sites. Therefore, plants are able to freely root through the surface organic layers and gain access to the nutrient-rich mineral horizons.

Dowding *et al.* (1978) report that most mosses in northern Alaska tundra sites require moist conditions as they derive their nutrients from water leaching from plants and litter rather than from soil. In this respect, the wet conditions of the Moss-*E. vaginatum* ct provide suitable habitat for bryophytes in terms of nutrient availability and, hence, contribute to the abundance of these plants in depressions.

5.5 Nutrients and Organic Matter

Shortages of available nutrients in the soil are frequently cited as responsible for the low rates of primary productivity in arctic tundra ecosystems (Billings and Mooney 1968, Bliss 1971, Ulrich and Gesper 1978). Nutrient input into the soil environment primarily depends upon release from weathering of soil parent material and upon release from decomposition of the organic part of the solum. Weathering and decomposition rates are slow in Arctic tundra ecosystems and, therefore, soil nutrient concentrations tend to be low in comparison to those of ecosystems in more temperate regions. Low concentrations of soil nutrients in tundra and forest-tundra sites have been reported by Heilman (1966, 1968) on the Alaskan North Slope,

Haag (1974) on the Pleistocene Mackenzie Delta, Babb and Whitfield (1977) on Devon Island, and Ulrich and Gesper (1978) at Barrow, Alaska.

Previous research on the role of nutrients in limiting tundra plant productivity has substantiated the hypothesis that both nitrogen and phosphorus are limiting for plant production. Marion and Miller (1982) reported that nitrogen is the most frequently limiting nutrient for the growth of tundra plants. Haag (1973) found that nitrogen was limiting in both upland and depressional sites on the Pleistocene Mackenzie Delta. Phosphorus was found to be limiting in lowland sites but not in uplands. Younkin (1972), working in the same area, found greater growth responses in native grasses with additions of phosphorus than with additions of nitrogen. Wet organic soils have been observed to be especially phosphorus deficient. Salisbury (1959) noted that phosphorus in combination with organic matter was not readily available to plants. Under conditions of high moisture content, phosphorus is highly subject to leaching loss due to its high solubility under reducing conditions (Glentworth 1949).

Besides the low nutrient status of arctic soils generally, there are usually substantial differences in nutrient availability within a single soil profile. Both Heilman (1966, 1968) and Janz (1974) showed that nutrient concentrations were substantially higher in the mineral portion of the solum compared to the organic portion. This difference was not evident on the involuted hill, probably due to the analytical procedure (see 3.2) rather than to a similarity in nutrient status.

In general, nutrient concentrations in the mineral part of the solum on the involuted hill did not differ significantly among the three ct's in which the thaw layer was deep enough to contact this horizon (see 5.3). Therefore, available nutrient differences among the ct's will be due to differences in the nutrient concentrations of the surface organic horizons. Nutrient inputs into these horizons will be limited by both moisture content and depth of the organic matter.

As outlined in 5.4, drier, aerated soils allow roots to penetrate into the nutrient-rich mineral horizons. The plants absorb these nutrients and subsequently release them into the organic horizons. By contrast, in saturated, anaerobic soils root penetration to the mineral horizons is inhibited or prevented altogether. As such, nutrient cycling is restricted and the nutrient status of the organic horizons will be poorer than in the drier soils.

Heilman (1966, 1968) and Janz (1974) clearly identify two limiting environmental conditions imposed on plant species occupying sites with deep accumulations of organic matter. The first effect of deep organic matter is on the depth of thaw. Soils in sites with deep peats are effectively insulated from the warmer overlying air and depths to frost are shallow. The combination of a deep peat and a shallow depth of thaw effectively reduces the amount of mineral soil in the solum. Smaller amounts of mineral soil are exposed to weathering and, therefore, these sites may show a deficiency in mineral-derived available nutrients.

The effects of organic horizon thickness on depth of thaw are illustrated as follows: the *S. glauca-L. arcticus* ct had thin surface organic horizons and deep thawed layers (Table 8). In this ct the mineral part of the solum typically occupied 85% of the soil profile in the thawed layer. By contrast, the *B. glandulosa-V. vitis-idaea* ct had thicker organic horizons, similar to the Moss-*E. vaginatum* ct (Table 8). In these 2 sites the mineral portion of the solum occupied only 40% and 35% of the thawed layer, respectively.

The Lichen-*L. palustre* ct had the thickest organic matter accumulations on the involuted hill. It appears that decomposition is severely limited in this ct, probably due to the extremely wet conditions in combination with cold soil temperatures created by the large ice-wedges. Such conditions would severely limit the activities of the soil micro-organisms responsible for decomposition. The deep peats of this ct effectively insulate the solum; the thawed layer was at its thinnest (23 cm) and the mineral portion of the solum was below the frost table.

The second effect of increasing accumulation of organic matter is that plants are increasingly cut off from the more nutrient-rich mineral portion of the solum. Heilman (1966, 1968), from work on north-facing slopes in interior Alaska, reported lower levels of nitrogen, phosphorus and potassium in the foliage of plants growing on thick peat compared to plants of the same species growing on thinner peats. He showed that nitrogen concentrations were high near the surface in mineral soils, but as organic matter accumulated, the zone

of maximum nitrogen content was concentrated in deeper, colder parts of the solum.

Haag (1972), from work on the Mackenzie Delta, showed how soil moisture and organic matter thickness, can be correlated with nutrient cycling in the solum. Upland sites, with thinner, drier, organic matter tend to have thicker active layers and more mineral soil is exposed to weathering. Weathering of the mineral horizons releases nutrients which become available to plants. The thin organic horizons allow for relatively easy access of roots to these weathered mineral horizons and cycling of the minerals can be quite rapid. The nutrient status of these sites is expected to be high. If so, shallow-rooted forbs such as _Pyrola_ spp. may find favourable habitats in upland sites not only because such sites are drier but because nutrients are more accessible.

Depressional sites with thicker organic matter have thinner thaw depths and less mineral soil exposed to weathering (Figure 5). Nutrient cycling is inhibited in the depressional stands and input of nutrients into the organic horizons is retarded. Some nutrients are recycled into the upper horizons, probably from deep rooting graminoids and runoff from upslope sites.

On the involuted hill nutrient concentrations in the organic horizons followed a pattern that is consistent with Haag's (1972) interpretation. Nutrient concentrations in the organic portion of the solum were highest in the upland tundra group which tended to have

soils with relatively dry, thin organic matter (Figure 5). Nutrient concentrations were lower in the soils of the depressional tundra group which had thick, wet surface organic horizons. The _S. glauca-L. arcticus_ ct has both dry soils and thin organic horizons. The more nutrient-poor _B. glandulosa-V. vitis-idaea_ ct also has dry soils but it has significantly thicker organic horizons. These thicker organic horizons will inhibit weathering of the mineral horizons and also restrict rooting into them. Thus, nutrient cycling is restricted, leading to a more nutrient-poor regime in the _B. glandulosa-V. vitis-idaea_ ct. Further research is needed to explain how these differences in organic matter depth arose in 2 ct's occupying the same topographic positions. One possible mechanism is that the _B. glandulosa-V. vitis-idaea_ ct's are an older stage in a successional sequence and that the deeper organic matter is due to a longer time period of accumulation.

Chapin _et al._ (1975) stated that plants with high respiration rates will have high nutrient requirements. High photosynthetic rates also demand high nutrient availability. It is, therefore, postulated that species with high respiration and/or photosynthetic rates will tend to be more prevalent in nutrient-rich sites. Species with lower metabolic rates will be able to exploit more nutrient-deficient sites. In general, spatial variations in soil nutrient availability, notably in the organic horizons, should strongly influence the distribution of ct's on the involuted hill.

While photosynthetic and respiration rates were not measured on

the plants of the involuted hill, research has been done on the same or related species from other tundra habitats. Pisek and Knapp (1959) report that deciduous shrubs have higher respiration rates than evergreen shrubs. Limbach *et al.* (1982), working in northern Alaska, reported that *Betula nana* assimilated carbon for photosynthesis at a high rate throughout its growing season, while *V. vitis-idaea* had a low photosynthetic rate. *Eriophorum vaginatum* had photosynthetic rates between the other 2 species.

Thus, from the literature, it may be inferred that both *Salix glauca* and *Betula glandulosa* have relatively high nutrient demands. The thin, dry, surface organic horizon is probably responsible for the maintenance of deciduous shrub species in the upland *S. glauca-L. arcticus* ct. The thin, organic horizons of the *S. glauca-L. arcticus* ct allow *S. glauca* and *B. glandulosa* to easily reach the mineral horizons and thus gain access to their required nutrients. Extrapolating from Haag's (1972) theory, because of efficient nutrient cycling in this ct, the organic horizons themselves may make significant contributions to the nutrient demands of these shrubs. In the B. *glandulosa-V. vitis-idaea* ct the cover of *Salix glauca* is lower. In this ct organic matter is significantly thicker, though not wetter, than in the *S. glauca-L. arcticus* ct. Because of the deeper organic matter, weathering may be inhibited and nutrients concentrated at greater depths in the *B. glandulosa-V. vitis-idaea* ct. These lower concentrations provide evidence that nutrient cycling is less effective in the latter ct. The fact that *S. glauca* is less common in the more nutrient-poor *B. glandulosa-V. vitis-idaea* ct provides

indirect support for the hypothesis that it is more sensitive to nutrient deficiencies than is B. glandulosa. Further research could involve determining the nutrient requirements of these 2 species as a first step in separating their niches in the upland tundra sites.

Heaths form a common and important element among ct's on the involuted hill. As mentioned above (5.4), heaths are classified as 'floaters' as their roots do not penetrate deeply into wet organic horizons. This shallow rooting system, while avoiding the problems of anaerobic soils, toxins, etc., makes the heaths susceptible to nutrient deficiencies. Heaths, however, exhibit special physiological adaptations which permit them to survive in nutrient-poor environments. Firstly, heaths are reported to have lower respiration and photosynthetic rates than forbs, graminoids and deciduous shrubs growing in similar habitats (Hadley and Bliss 1964, Johnson and Tieszen 1976). With lower levels of metabolic activity, heaths will require smaller quantities of nutrients and will, therefore, be able to survive in nutrient-poor environments. Secondly, older leaves on these species were found to have lower net photosynthesis, lower respiration rates, and higher lipid contents than new leaves (Hadley and Bliss 1964, Johnson and Tieszen 1976). It has been suggested that these old leaves act as nutrient storage elements (Hadley and Bliss 1964), an adaptation analogous to the storage role of rhizomes in herbaceous perennials. Thus it appears that heaths have both a relatively low nutrient requirement and further that they are efficient in conserving the nutrients that they accumulate. These adaptations enable the heaths to survive in nutrient-poor

environments.

The presence of thick organic horizons in combination with very wet conditions will inhibit the development of shrub-dominated communities in the depressional sites. Janz (1974) reached the same conclusion. Plants growing in the Moss-*E. vaginatum* and Lichen-*L. palustre* ct's show a number of special adaptations to their environment in which nutrient cycling is restricted and the nutrient-rich mineral horizon is buried beneath a thick, wet, surface organic horizon.

Both Johnson and Tieszen (1976) and Limbach *et al.* (1982) have reported that in arctic Alaska, graminoids have photosynthetic and respiration rates between those shown by evergreen and deciduous shrubs. As deciduous shrubs are uncommon in depressional sites, graminoids are probably the most nutrient-demanding species in these habitats. Chapin *et al.* (1975) have established that these tundra graminoids have the ability to concentrate nitrogen, phosphorus and potassium to levels significantly higher than in comparable temperate species. Furthermore, prior to leaf senescence, nearly half of the above ground complement of these nutrients is translocated from the leaves to the rhizomes rather than lost to the soil (Chapin *et al.* 1975). The ability to concentrate and retain nutrients aids graminoids in occupying the nutrient-deficient Moss-*E. vaginatum* ct.

The ability of *Eriophorum vaginatum* and *Carex bigelowii* to produce deep roots that penetrate the thick, anaerobic, organic horizons

further improves their ability to survive in depressional sites. In northern Alaska cottongrass tussock tundra sites, with organic horizons up to 30 cm thick, less than 5% of below-ground live phytomass penetrated to the mineral portion of the solum. The two exceptions were *E. vaginatum* and *C. bigelowii*. These two species had up to 26% and 62%, respectively, of their live root mass in the mineral part of the solum in these deep organic sites (Shaver and Cutler 1979). As mineral cycling is retarded in depressional sites the ability to produce roots that can penetrate deep organic soils allow these sedges access to available nutrients from the mineral horizons. This enhances *E. vaginatum's* ability to dominate in the Moss-*E. vaginatum* ct.

Eriophorum vaginatum is rare in the Lichen-*L. palustre* ct, which does not include the mineral portion of the solum within the thawed layer (Figure 5). Thus despite its ability to withstand water-saturated soils with thick organic horizons, it appears that *E. vaginatum* requires some minimal amount of nutrients which are only available from a thawed mineral horizon.

Neither mosses nor lichens can absorb nutrients directly from the soil. They absorb nutrients from precipitation and from the water which leaches from vascular plants and litter (Dowding *et al.* 1981). Thus the distribution of mosses and lichens do not directly depend upon soil nutrient availability. Nutrients may be most available to the mosses where snow melt water effectively leaches dead standing material of nutrients (Dowding *et al.* 1981). Therefore, on the

involuted hill, mosses are most abundant in the depressions where they can receive snow melt water. The relatively low cover of mosses in the Lichen-L. palustre ct is probably due to the slightly elevated microrelief created by high-center polygons. The centers of these polygons will be free of snow (Corns 1974), thereby not only exposing mosses to desiccation but also depriving them of necessary nutrients from snow melt and leaching. Similarly, the relatively snow-free upland ct's will have low amounts of nutrients available for mosses. The low cover of bryophytes in the upland ct's may be due, in effect, to nutrient deficiencies.

Lichens are also unable to absorb nutrients directly from the soil. They derive their nutrients from rainwater (Hale 1974) and snow meltwater. It is to be expected, therefore, that lichens will be prevalent in more open sites where there is little interception of precipitation from an overhanging vascular plant canopy. The extremely poor soil nutrient regime of the Lichen-L. palustre ct, coupled with the deep, wet organic material limits the development of shrubs. The open condition of this ct creates a habitat where precipitation can reach the soil surface, thereby resulting in optimal conditions for the development of lichens.

Variations in available nutrients and the rate of nutrient cycling between ct's probably plays a significant role in the distribution of ct's on the involuted hill. Differences in organic matter depths, which are correlated with habitat types, strongly influence the rate of nutrient cycling and, in combination with soil moisture content,

determine nutrient availability to plants.

Upland tundra stands typically have relatively dry, thin organic horizons which tends to create a rapid rate of nutrient cycling and greater nutrient availability. Thus upland sites can support the more nutrient-demanding forbs and deciduous shrubs. By contrast, depressional stands have wetter, thicker organic horizons; nutrient cycling is hindered and nutrient availability is low. These stands support species that are less nutrient-demanding and/or are more efficient in retaining nutrients (e.g., *Eriophorum vaginatum*, *Ledum palustre*).

6.0 SUMMARY AND CONCLUSIONS

1. Involuted hills are concentrated in a 500 sq km area which starts about 15 km east of the hamlet of Tuktoyaktuk on the Pleistocene Mackenzie Delta. The hills are massive ground-ice landforms on which there are a series of large ridges, creating a "wrinkled" landscape. Geological evidence suggest that this area was not covered by the late-Wisconsin glaciation and hence may have been ice-free for at least 40,000 years.

2. The objectives of the study were to: (1) provide a classification of the plant community types (ct's) which occur on the involuted hill, (2) relate the ct's on the involuted hill to ct's found in other low arctic regions, and (3) attempt to provide some insight into edaphic factors affecting the distribution of the ct's on the involuted hill.

3. Using minimum variance cluster analysis, principal components analysis and field observations, the 34 stands sampled quantitatively on the involuted hill were classified into 5 ct's within 3 major groups.

   a) Upland Tundra Group - This group occupies the large outer ridges of the hill, midslope positions and rims of the large ice-wedges which occur on the central plateau. Both ct's in this group are dominated by deciduous shrubs. The 2 ct's in this group are the *Salix glauca*-*Lupinus arcticus* ct and the

Betula glandulosa-Vaccinium-vitis-idaea ct.

b) Depressional Wetland Tundra Group - These communities occupy depressional sites where the water is stagnant. The group is composed of 2 ct's: the Moss-*Eriophorum vaginatum* ct occurs in depressions between the outer ridges of the hill and in smaller ice-wedge polygon depressions; the Lichen-*Ledum palustre* ct occurs on well-developed, high-center polygons and in snowpack sites.

c) Lotic Wetland Tundra Group - This group is found only along drainage channels which dissect the outer ridges of the involuted hill. Water flows through these channels all summer. A single deciduous shrub community, the *Salix pulchra-Alnus crispa* ct, makes up this group.

4. All the ct's found on the involuted hill have been reported from other low arctic regions in North America. What is exceptional about the involuted hill is that it has ct's reported from both the Arctic Coastal Plain and Foothills Provinces. Most areas of coastal lowland tundra are dominated by ct's similar to the Moss-*Eriophorum vaginatum* ct or the Lichen-*Ledum palustre* ct, with shrub-dominated ct's being rare or absent. The prevalence of shrub-dominated ct's on the involuted hill gives it a physiognomy characteristic of the Foothills province on the Alaskan North Slope. It thus appears that the uplands of the involuted hills contain disjunct foothill elements.

5. In the Upland Tundra Group earth hummocks and disrupted soil profiles are common; all soils have a mineral base. All upland soils belong to the Turbic Cryosol great group. Soils from 3 Turbic Cryosol subgroups are found in the Salix glauca-Lupinus arcticus ct: Brunisolic, Orthic and Gleysolic. The Betula glandulosa-Vaccinium vitis-idaea ct is dominated by Brunisolic and Orthic Turbic Cryosol subgroups.

6. Earth hummocks and disrupted horizons are less common in Depressional Tundra stands. In the Moss-Eriophorum vaginatum ct the mineral horizon is gleyed, reflecting the wetter, anaerobic conditions. Soils of this ct are dominantly Gleysolic Static Cryosols with minor inclusions of Gleysolic Turbic Cryosols. In the 3 stands of the Lichen-Ledum palustre ct that developed on high-center polygons, organic horizons occupied the entire active layer. Soils in these stands are probably Mesic or Humic Organic Cryosols. Soils were not sampled in the snow bank stands and the Salix pulchra-Alnus crispa ct.

7. Soil moisture content was significantly greater in the Depressional Tundra Group than in the Upland Tundra Group. There was no significant difference in soil moisture content within each group. Organic depths tended to be thinnest in the Salix glauca-Lupinus arcticus ct and thickest in the Lichen-Ledum palustre ct. The depth of organic matter was intermediate and equal in the Betula glandulosa-Vaccinium vitis-idaea ct and the Moss-Eriophorum vaginatum ct. Mineral soil in the active layer

was thickest in the *S. glauca-L. arcticus* ct, intermediate in the B. *glandulosa-V. vitis-idaea* ct and Moss-*E. vaginatum* ct, and did not appear in the Lichen-*L. palustre* ct.

8. In general, available nutrient concentrations in the mineral part of the solum were uniform among the ct's. In the organic horizons available nutrients, notably nitrogen, phosphorus and calcium, tended to be greater in the Upland Tundra Groups than in the Depressional Tundra Groups. The ct's, in order of decreasing available nutrient content in the organic horizons, are: *S. glauca-L. arcticus*, *B. glandulosa-V. vitis-idaea*, Moss-*E. vaginatum*, Lichen-*L. palustre*.

9. Soils in depressional sites are waterlogged and probably anaerobic. Thus plants that are able to translocate oxygen from their shoots to their roots (e.g., *E. vaginatum*) or that can root above the anaerobic portion of the solum (e.g., most ericaceous shrubs) will be able to survive in depressions. The drier soils of the Upland Tundra Group allow plants to freely root through the surface organic horizons.

10. Nutrient availability is a major factor determining the location of the ct's on the involuted hill. Both *Salix glauca* and *Lupinus arcticus* are restricted to the stands of highest nutrient availability on the hill. These stands have thin organic horizons, deep thawed layers and relatively dry, but not xeric, soil moisture regimes. Such stands will have more rapid nutrient

cycling and can support the more nutrient demanding deciduous shrubs and forbs. The fact that the cover of _S. glauca_ is lower in the _B. glandulosa-V. vitis-idaea_ ct, where soil moisture is not significantly different than in the _S. glauca-L. arcticus_ ct, but organic matter is deeper and more nutrient-poor, may indicate that nutrient availability limits the distribution of _S. glauca_ on the involuted hill.

11. Depressional stands are dominated by species adapted to the low nutrient availability in these sites. These species have low nutrient requirements and/or are efficient in retaining the nutrients they absorb (e.g. _Ledum palustre_, _Eriophorum vaginatum_).

12. Neither mosses nor lichens can absorb nutrients directly from the soil. They survive in the nutrient-poor depressional stands by absorbing nutrients from precipitation and from water leaching from vascular plants and litter. On the involuted hill mosses are most abundant in depressions where they can obtain water from melting snow. Lichens are prevalent on high-center polygons. These polygons are extremely low in available nutrients, restricting the development of a vascular plant canopy. As there is little interception of precipitation by vascular plants, lichens thrive in these open sites.

13. Although no soils data are available for the _Salix pulchra-Alnus crispa_ ct some qualified speculations can be made about the occurrence of this ct. Nutrient availability is probably high in

this ct as the flowing water is likely bringing in nutrients from the upland sites and may itself be eroding into the mineral soil. A high nutrient availability and oxygen supply would explain the abundant and vigorous shrub growth observed in this ct. As water is flowing through these stands it may not produce the problems associated with the stagnant water of the depressional stands. This would further allow for the dominance of shrubs in these habitats rather than graminoids.

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8.0. APPENDIX I. Similarity coefficient matrix of the stands on the involuted hill study site.

S 2	32.143													
S 3	21.733	46.664												
S 4	14.519	13.179	23.146											
S 5	19.875	48.684	2.154	21.381										
S 6	39.465	3.056	49.406	18.757	52.725									
S 7	27.496	29.959	11.291	17.717	12.887	29.141								
S 8	18.373	14.355	41.977	8.397	39.055	22.056	40.472							
S 9	26.287	50.261	2.821	25.041	3.583	55.889	14.484	45.485						
S 10	19.958	17.107	40.167	15.855	39.010	21.976	39.618	9.826	45.977					
S 11	25.423	46.484	4.799	24.715	6.523	50.241	17.049	41.939	1.832	42.219				
S 12	21.120	11.975	45.121	6.191	42.955	21.777	39.026	6.380	45.749	20.566	43.829			
S 13	16.735	5.043	29.459	5.725	30.821	7.375	20.275	8.690	34.464	8.937	31.304	10.283		
S 14	34.938	3.957	40.515	12.862	41.535	4.437	25.322	14.845	44.932	12.204	41.586	18.747	5.708	
S 15	47.843	85.999	19.807	51.684	17.214	89.690	42.383	69.038	12.784	72.137	10.434	75.593	63.937	77.132
S 16	23.076	16.714	52.811	13.867	52.819	28.603	48.210	12.997	53.867	25.663	52.048	4.668	13.575	28.350
	86.486													
S 17	45.198	14.966	35.983	15.880	37.126	20.316	16.461	34.044	33.917	37.866	37.062	24.538	18.174	14.854
	72.644	32.614												
S 18	19.174	23.124	62.361	27.622	60.914	33.921	64.002	14.398	67.146	14.882	62.078	17.403	20.081	31.750
	95.885	15.892	57.346											
S 19	23.604	47.527	1.840	25.005	3.383	49.248	15.251	42.679	2.808	39.816	2.329	46.455	30.974	40.781
	12.913	55.858	39.864	61.845										
S 20	17.565	10.183	19.458	7.452	21.135	9.930	15.200	13.404	26.152	10.788	23.650	17.346	3.842	6.753
	52.420	25.403	19.968	27.356	19.859									
S 21	38.756	16.641	35.073	27.027	37.050	13.667	16.676	39.057	40.030	30.678	39.267	40.622	15.783	14.982
	71.820	44.127	19.471	49.197	36.989	14.671								
S 22	19.966	46.461	6.057	25.452	7.157	47.852	7.242	47.810	9.694	44.623	12.531	47.809	28.790	43.251
	31.486	51.569	35.299	63.359	9.997	22.972	28.681							
S 23	36.907	23.745	21.389	20.556	23.872	18.649	4.652	39.523	26.639	34.985	26.131	41.404	17.813	16.502
	54.726	53.536	17.588	64.403	23.312	12.164	12.661	18.808						
S 24	27.136	33.915	8.829	21.121	10.594	32.296	5.309	43.671	13.452	40.272	15.274	41.654	22.791	29.430
	38.800	49.252	24.036	62.131	11.382	14.752	19.705	5.124	10.861					
S 25	10.526	31.700	43.106	20.977	42.913	43.581	48.250	20.456	46.522	21.483	45.307	18.340	18.914	40.769
	74.360	10.040	50.273	12.219	46.224	27.628	46.345	39.412	57.990	46.302				
S 26	79.647	104.790	67.313	75.421	59.656	106.532	76.896	87.009	69.523	97.863	73.867	91.663	88.497	96.763
	63.362	107.076	97.859	115.219	63.019	73.691	102.712	74.695	84.971	71.338	105.974			
S 27	19.128	3.756	39.261	10.774	40.619	8.652	29.761	10.597	43.411	9.678	40.142	9.726	3.062	7.761
	76.583	11.102	21.048	12.068	40.263	7.922	18.271	37.500	27.364	29.635	16.442	96.299		
S 28	55.663	88.034	20.634	61.003	24.948	91.017	43.275	83.652	13.641	81.437	9.482	85.341	68.289	82.649
	10.476	91.442	73.241	103.224	14.949	57.575	71.122	30.892	55.151	37.657	78.105	104.194	78.986	
S 29	38.511	64.320	10.920	40.148	13.577	66.079	21.691	64.064	6.036	64.282	3.707	63.492	47.018	60.117
	10.990	70.453	48.969	85.326	7.975	39.123	48.165	14.413	32.723	19.716	61.361	88.060	57.739	4.608
S 30	23.373	48.968	16.765	33.580	18.037	46.684	16.180	48.246	24.980	31.243	25.135	59.707	28.747	39.440
	45.864	64.323	49.621	59.110	19.630	22.356	27.787	11.256	19.023	17.295	43.244	90.274	38.422	46.772
	30.591													
S 31	21.774	11.890	41.256	10.504	39.610	13.513	30.286	12.973	45.557	27.430	41.603	8.840	9.893	18.207
	70.751	15.487	28.739	24.897	41.462	13.307	26.704	39.787	29.305	31.606	27.840	85.062	11.823	80.305
	56.237	50.865												
S 32	31.145	66.921	7.824	37.486	8.333	71.814	19.811	61.210	3.983	59.484	4.973	61.722	46.485	61.992
	12.085	67.251	49.019	80.559	7.538	39.323	49.971	9.029	34.506	18.342	52.966	81.321	56.889	9.832
	3.191	23.372	59.241											
S 33	56.855	68.694	46.149	52.199	43.919	64.425	46.493	64.196	52.924	59.007	52.643	73.929	53.568	57.549
	61.853	87.500	69.792	87.386	43.818	41.982	59.217	49.711	45.818	45.331	81.381	56.306	63.632	82.163
	64.695	47.570	63.306	61.803										
S 34	18.612	5.974	35.887	3.894	35.869	10.684	27.404	6.335	39.201	11.884	36.448	3.735	2.445	8.634
	69.135	8.204	18.579	17.960	37.008	7.257	24.677	36.831	25.982	28.968	18.034	87.242	3.679	75.868
	54.141	41.811	7.024	53.706	60.066									